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The Victorian Era Series

The Science of Life

The
Science of Life

An
Outline of the History of Biology and its Recent Advances

By

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BLACKIE AND SON LIMITED
50 OLD BAILEY LONDON
GLASGOW AND BOMBAY

Preface

This little book bears a big title—The Science of Life—which is synonymous with Biology. Such a title would be unjustifiable did not the position of the book in the Victorian Era Series show that it is intended simply as a historical sketch of the evolution of the science, especially in Darwinian and post-Darwinian days. It is an attempt to illustrate the growth of Biology from an embryonic state of insignificance to a position which is central among the sciences, and full of influence even on the art of life. By reference to particular problems, and occasionally by reference to particular men, I have tried to illustrate impartially what may be called the modern biological attitude.

In most of the chapters I have begun the story before the Victorian Era; it did not seem possible to understand the historical position without so doing.

Although I have for many years burrowed not a little in the literature of Biology, even this inadequate sketch would have been impossible without the help of various historical surveys which have appeared from time to time, notably the

History of Zoology by Carus and the *History of Botany* by Sachs. But neither of these extends beyond Darwin's day.

If I might venture to associate this little book with a great name, I should dedicate it with much gratitude to one of my teachers—Ernst Hæckel—whose life has been so closely bound up with the advancement of modern Biology.

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Foundations.

Although the inquisitive mood is probably instinctive in man, it does not seem likely that the early conditions of human life can have favoured the pursuit of knowledge for its own sake. It was doubtless in practical lore that the science of life had its beginnings. The gardener and the shepherd, the herb-gatherer and the huntsman, were the pioneers of the biologist, and they may teach him still.

If we use the term Biology, in its widest sense of Life-lore, to include all the results of the scientific study of living creatures, we must admit that it had its foundations in antiquity. But if we restrict the word, as is often done, to the study of the general vital phenomena common to plants and animals, then it is very modern. A long period of descriptive work and detailed analysis was necessary before there could be much progress with the general problems of biology (in the stricter sense), which have to do with the nature and origin, continuance and evolution, of organic life. Even the word Biology is not older than the beginning of the nineteenth century.

Of the period before Aristotle it is perhaps enough to say that it reminds one of childhood—the useful, the dangerous, the strange bulked largely in men's minds;

inquisitiveness was strong but uncritical, and even round the simplest facts the intellectual fingers failed to meet.

Aristotle.

But just as there are precocious children, so there was an early naturalist, whose works represent the most remarkable achievement of any one thinker. The foundations of biology were laid by Aristotle (384–322 B.C.). He collected and classified, dissected and pondered, and the prevision of his insight reached forward to generalizations which were not established till two thousand years had passed.

The Dormant Period.

Aristotle laid firm foundations, but for fifteen centuries they remained unbuilt upon, and were indeed in great part obscured by accumulations of rubbish. Apart from a few exceptions, such as Pliny (23–79 A.D.), a diligent but uncritical collector of facts, and the physician Galen (130–200 A.D.), who had the courage to dissect monkeys, men were preoccupied with the practical tasks of civilization, alike in peace and war, and science slumbered.

Legendary Biology.

Even during the dormant period there were never lacking those who, as it were, dreamed of the great world around them. Their dreams are expressed in such literature as the famous *Physiologus*, which is found in about a dozen languages and in many forms, partly a collection of natural history fables and anecdotes, partly a treatise on symbolism, and partly an account of the medicinal and magical uses of animals. Fact and fiction were in those days inextricably jumbled; credulity ran riot along the paths where the scientific method afterwards established order; and the dominant theological mood affected even the vision of those who tried, as some did, to get away from tradition and back to nature.

The Scientific Renascence.

It would be a difficult task to state in due proportion all the factors which contributed to the scientific renascence. It came about gradually: and, as in the making of the butterfly out of the chrysalis, processes of disruption went hand in hand with reconstruction. The freer circulation of men and thoughts associated with the Crusades, the widening of the horizon by travellers like Columbus,

the founding of universities and learned societies, the establishment of museums and botanic gardens, the invention of printing and the translation of Aristotle's works—these and many other practical, emotional, and intellectual movements gave fresh force to science, and indeed to the whole life of man.

The Encyclopædists.

As far as biology was concerned, the direct result of the scientific renascence might be described as a return to nature. It began to be perceived that Aristotle had not quite finished the subject, and that every man might be his own observer. With enthusiasm men turned to the task of seeing for themselves, and there began the period of the Encyclopædists. This somewhat cumbrous title is useful, for it suggests the omnivorous habits of those early workers, who, with an appetite greater than their power of digestion, collected all possible information about all sorts of living things. Prominent among them were four: the Englishman Edward Wotton (1492–1555), who wrote a treatise, *De Differentiis Animalium*, still in great part Aristotelian; the Swiss Conrad Gesner (1516–1565), author of a voluminous *Historia Animalium*; the Italian Aldrovandi (b. 1522); and the Scot Johnston (b. 1603).

Although Buffon was a thinker, it seems almost fair to say that the best aims of the Encyclopædists were realized in his *Histoire Naturelle*, which appeared in fifteen volumes between 1749 and 1767. He may be taken as the centre of a strong enthusiasm for natural history which characterized a great part of the eighteenth century, and found expression in the brilliant discoveries of workers like Réaumur, Rœsel, De Geer, Schäffer, and Bonnet.

From Buffon to Darwin.

Buffon took all nature for his province; but from his date we have, apart from a few great workers, to deal with specialists, becoming more and more specialized as we approach to-day. Thus there is a marked division between the investigators of form and structure (morphologists) and the investigators of habit and function (physiologists). There have been, and are, many who may be cited as both, but the moods and methods of the two disciplines are quite different.

The morphologist asks the question, "*What is this?*" and analyses, anatomizes, the dead; the physiologist asks the question, "*How is this?*" and analyses the living. The parallelism of these two inquiries, from Buffon to Darwin, has been luminously expounded by Prof. Patrick Geddes, and we follow his exposition.

A. MORPHOLOGICAL ANALYSIS.

(1) THE ORGANISM.—The morphologist naturally begins by describing the external characters of the intact creature—its symmetry, shape, architectural plan, and the like; and with the beginning of this we must associate the work of Ray and Linnæus. The work is still in progress, for "each new species described means a leaf added to the *Systema Naturæ*".

(2) THE ORGANS.—The description of superficial characters is, however, only the beginning of morphology; an analysis of organs is the next step. This may be especially associated with the name of Cuvier as zoologist, and Jussieu as botanist. This task is also an unending one, "to which every new descriptive anatomical research belongs as clearly as if it were published as an appendix to the *Règne Animal* itself".

(3) THE TISSUES.—The next logical step was taken in 1801 by Bichat, who in his *Anatomie Générale* analysed the body into its component tissues. This was the beginning of histology, which has now so many devotees.

(4) THE CELLS.—Minute analysis could not remain long at the level of tissues; these were soon analysed into their component or originative cells, the nucleated corpuscles of living matter which form the basis of all organic structure. This step must be particularly associated with Schwann and Schleiden, who formulated the "Cell Theory" in 1838–39. With the study of cells hundreds of modern workers are more or less exclusively occupied.

(5) PROTOPLASM.—The fifth and last step in morphological analysis, within the limits of biology, is that which passes from the cell as such to a study of the living matter and other substances which compose it. With this, though it is difficult to select names, the work of Dujardin, Von Mohl, and Max Schultze may be associated.

B. PHYSIOLOGICAL ANALYSIS.

(1) HABITS OF THE ORGANISM.—The early physiology was largely concerned with the ways and habits of the intact creature, sometimes rising to invaluable studies in "Natural History" or

"Bionomics", but again falling into verbal disquisitions on "spirits" and "temperaments".

(2) FUNCTIONS OF ORGANS.—As the anatomists, scalpel in hand, disclosed the intricate mechanism of the living engine, the physiologists were bound to follow, and the study of the functions of organs began. Harvey's investigation of the heart was an early type of this kind of work, and Johannes Müller may be noted as one of the first to broaden the study by making it comparative.

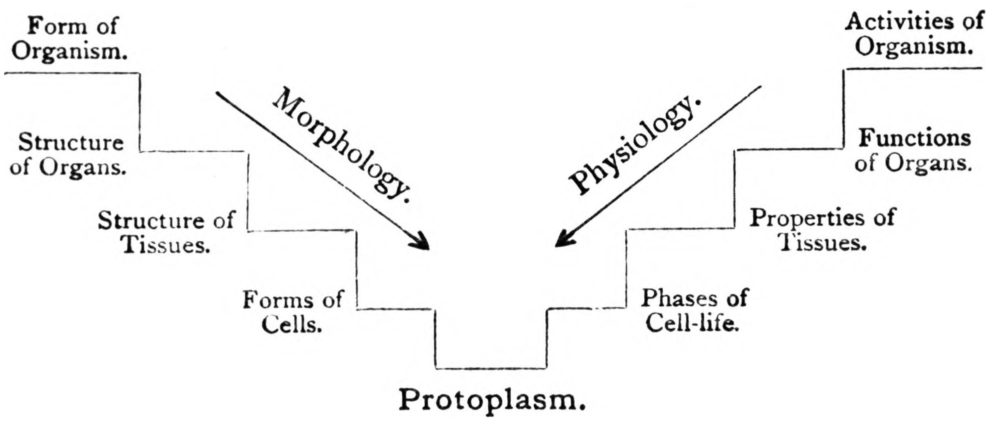
(3) PROPERTIES OF TISSUES.—Bichat was physiologist as well as morphologist, and sought to express the functions of an organ, like the heart, in terms of the properties of its component tissues. He thus "not only deepened both morphology and physiology by a new analysis, but showed them to coincide in the study of tissue".

(4) PHASES OF CELL-LIFE.—What has been said of Bichat may also be said of Schwann, for there was a physiological side to his cell-theory, namely, the idea, as Prof. E. Ray Lankester states it, "that the differences in the properties of the different tissues and organs of animals and plants depend on a difference in the chemical and physical activity of the constituent cells, resulting in a difference in the form of the cells, and in a concomitant difference of function". The same idea was suggested by Goodsir, and developed in relation to pathology by Virchow.

(5) METABOLISM OF PROTOPLASM.—But even in Schwann's mind the early preoccupation with the cell as such gave place to a proper estimate of the protoplasm itself. Herein the history of physiology shows what Prof. Michael Foster has called "a change of front". The riddle of life has henceforth to be read, as far as may be, in terms of the chemical changes (metabolism) associated with the living matter.

Prof. Geddes's short paper emphasizes the parallel evolution of the two sides of biological science, and rationalizes the history as a logically progressive analysis. From external form to the internal organs, from organs to the tissues which compose them, from tissues to their elementary units or cells, and from cells to the living matter itself, has been the progress of the science of structure or morphology. From habit and temperament to the work of organs, from the functions of organs to the properties of tissues, from these to the activities of cells, and from these finally to the chemical and physical changes in the living matter or protoplasm,

has been the parallel progress of the science of function or physiology. This may be diagrammatically expressed.



"Or we may conceive the diagram as representing a double series of five shelves, on which the literature of the different planes of research is disposed."

Morphology.		Physiology.
Linné.	Organism	Haller.
Cuvier.	Organ	Müller.
Bichat.	Tissue	Bichat.
Schwann.	Cell	Virchow.
Dujardin.	Protoplasm	Bernard.

It may seem to some that much of biology is ignored in this brief sketch of morphological and physiological analysis. But there are fewer omissions than there seem to be.

What of Palæontology and Embryology, what of the old-fashioned Natural History and the modern Ætiology? Taking the last first, it is hardly a department of biology, it is a way of looking at *all* biological facts.

No piece of work in morphology or physiology is complete until it is seen in its ætiological or evolutionary aspects. "Evolution bears, in fact, the same relation to morphology and physiology as history to statistics."

As to the old-fashioned "Natural History" or the new-fashioned "Bionomics", that is eminently physiological; the habits of the organism, the behaviour of mates, the ménage of the family, the competition and co-operation among fellows, the struggle for existence in its widest sense—the study of these is physiological, just as classification or the working-out of genealogical trees is morphological.

As to Embryology, it has been until recently almost wholly morphological—the study of stages in the growing organism, in the developing organs, in the differentiating tissues, in the lineage of cells. To this, quite recently, there has been added some physiological analysis of the actual processes at work in the development.

Finally, as to Palæontology, this is strictly morphological—the anatomy, perhaps even the histology, of the extinct. That both palæontology and embryology have become what might be called historical or genealogical in their aims, is wholly due to the influence of the evolution doctrine. Palæontology had not this meaning to Cuvier, nor embryology to Wolff.

But to infer from this summary that the history of biology for the last hundred years and more has been a steady and orderly progress in scientific analysis would be an entire misunderstanding. Since the beginning of the Victorian era, at least, there has been contemporaneous work on all the five lines, and many a worker has been at once morphologist and physiologist, at several levels of analysis. Moreover, it must be remembered that a retrospect of progress from a vantage-ground of achievement is apt to see a definiteness in the various movements which those who shared in them were but dimly aware of. And, finally, we must recognize that while to-day's description of the externals of a new species may be called a Linnæan piece of work, and a modern anatomical paper Cuvierian, and so on,

this is not the full statement, for the species-maker of to-day has in most cases a conception of species very different from that of Linnæus, and the so-called modern Cuvierian is now, in most cases, aware that he is deciphering the structural record of genetic affinities. The evolution doctrine has altered the tone of work at all the levels of analysis; and what is true of this greatest generalization is true of some of the minor ones as well.

It would be interesting to define precisely what are the characteristics of *modern* work in the different departments of biology. But the task is a very difficult one. Since Darwin began to sway the minds of biologists there have been many changes, some of them directly, others indirectly, due to his influence. It is probable that the main currents of progress will be clearer a hundred years hence than they are to those within their sweep, and it may be that some ideas which now appear of doubtful survival value will afterwards become of paramount importance.

After Darwin.

As the result of evolutionary views, classification has tended to become a record of pedigrees. Not that the pre-Darwinian classifiers failed to look for, or to find, natural affinities, but the doctrine of descent has invested these with new meaning. We may associate the change with the name of Hæckel, who championed genealogical trees in the days of early unpopularity.

The change in morphological work may perhaps be generally expressed by saying that it has acquired an evolutionary purpose. A piece of "pure anatomy" may be part of a necessary discipline, and it is always possible that it may fill a vacant niche; on the other hand, its value may be altogether *quantitative*. A perception of this has tended to favour work which imitates Gegenbaur's rather than that which remains Cuvierian. As Prof. E. Ray Lankester says, "Pure morphography has long since ceased to be a principal line of research".

In the domain of histology, the most striking feature has been the concentration of research on the problems of cell-division (E. van Beneden, Boveri, O. Bütschli, W. Flemming, O. and R. Hertwig, and many others).

The demonstration of the marvellously exact bipartition of nuclear elements; the discovery of the centrosomes, which *appear* to act as dynamic centres in cell-division; the experimental proof that a cell bereft of its nucleus may move and feel for a time, but cannot assimilate or secrete; and the growth of criticism as to the adequacy of the cell-theory, may be noted as representative steps in modern cytology.

In regard to development, the most momentous step has been the recognition of germinal continuity. The unique potentiality of the germ-cells depends upon their continuity through successive cell-generations with the germ-cells of the parent organism. We may associate this doctrine with the name of Weismann.

Also of great importance is the renewed attack on the problems of physiological embryology, and the discovery of some ingenious experimental methods, in connection with which the names of Roux and O. Hertwig are especially prominent. And although no answer is yet forthcoming, there has been a clearer statement than heretofore of the fundamental question: Is the path of embryonic development definitely predetermined in the organization of the germ-cells; or is the path, so to speak, mapped out, as development goes on, by the varied relations and conditions to which the embryonic cells are exposed?

Palæontology has risen to high dignity as a branch of biology, its results being now universally recognized as the surest contributions to the history of life upon the earth. The distinction between the anatomist and the "fossilist" has disappeared, both being now equally morphological and evolutionary. We may connect the change with the name of Zittel.

Among the characteristics of modern physiology we may notice the slow but important development of comparative work, with its evidence that there is unity amid diversity in vital processes; the increased concentration on the problems of metabolism (the chemical changes of the living body); the application of physiological results and methods to the problems of development; and the rise of a school of "neo-vitalists", who have helped to

save the science from self-conceit by their emphasis on the partial nature of all physiological analysis.

Bionomics has risen in dignity by a realization of its evolutionary importance. From being an emotional student of habits, or an inquisitive collector of the "curiosities of animal life", the open-air observer and explorer has become an important contributor to the theory of adaptation and struggle, or to animal psychology.

In regard to heredity, the most important steps have been: (*a*) The formulation of the doctrine of the continuity of the germ-plasm (Weismann); (*b*) The growth of scepticism as to the transmissibility of acquired characters (Weismann); (*c*) The accumulation of evidence pointing to the conclusion that the chromatin of the nuclei is the chief bearer of hereditary qualities (Hertwig), and the proof that the chromatin of the fertilized egg-cell consists in equal parts of paternal and maternal chromatin, which are equally distributed in the subsequent cell-divisions; and (*d*) The law of ancestral inheritance, due to Galton.

In regard to the primary or originative factors in evolution, those namely which give rise to variations, some progress has been made, though the problems are still far from solution. (1) Some clearness has been gained by defining the distinction between congenital *variations* due to changes in the germinal substance and *modifications* which are wrought upon the body as the results of change in function and environment. (2) Some excellent experimental work has been done in the artificial production of modifications. (3) A great service has been rendered by Mr. Bateson in his *Materials for the Study of Variation*, which contains an exhaustive account of observed instances of a certain kind of variation, and affords some evidence of the occurrence of what is called "discontinuity" in evolution. (4) The statistical study of variations, developed by Mr. Galton and Profs. Weldon and Pearson, marks the introduction of a new method, which aims at representing in a curve the extent of variation in a given character, and the proportion of individuals exhibiting it.

As regards the secondary or directive factors in evolution, attempts have been made to give statistical evidence of the action of selection or elimination (Weldon, Pearson); many detailed illustrations have been furnished as to the utility or survival-value of trivial characters; the content of the phrase "struggle for existence" has been enlarged; and the importance of various forms of "Isolation" has been suggested (Romanes, Gulick).

Great improvements in technical methods have made analysis much more thorough. The microtome has enabled us to dissect an animal in a new way—in a continuous series of fine sections—from which, if necessary, an accurate model can be reconstructed. A young student may now make better sections than was possible to Huxley. Countless methods of rapid fixing and differential staining have greatly aided the investigation of minute structure, and some attempt has even been made to understand the chemistry of the changes. The "method of Golgi" and its rivals have entirely altered the aspect of neurology. The apochromatic lenses mark an epoch in the evolution of the microscope. But a volume would be needed to do justice to the influence of methods on the progress of biology.

Summary.

This outline will become clearer if it be re-read after the other chapters, but its drift may be shortly summed up. The history of biology before Darwin shows a progressive analysis of structure and function; the progress of biology after Darwin shows the increasingly penetrating influence of the evolution-idea, the growth of a more critical and cautious scientific spirit, a perfecting of methods of research, and tentative suggestions towards the synthesis which must succeed analysis. From different sides the minds of all are turned towards the problem of constructing a working thought-model of the organism in its individual development, in its racial history, and in its everyday activities.

Chapter II.

Classification of Animals.

Meaning of Classification—Early Classifications—Physiological Classification—Aristotle—Ray and Linnæus—Lamarck—Cuvier—Recognition of Embryological Basis—Genealogical Trees—Grades of Classification—Conception of Species.

The word *classification* is apt to sound dull to many ears, yet it is doubtful whether there is any exercise more irresistible or more fascinating. Is there anyone, until he has realized the fallacy of it, who does not feel ill at ease until he has classified his neighbours, as rich or poor, as ignorant or cultured, as socialists or anarchists, and so on through the list of groups which have at least some of the distinctions of species?

Meaning of Classification.

Do we not see our children slowly working out their *taxonomy* of herb, shrub, and tree; of beast, bird, and creeping thing; or better than these, unless the pleasure of it be too ruthlessly denied them? Do they not in some measure recapitulate the history of classifications, advancing from the artificial to the natural, from the utilitarian to the scientific? Are they not, in the Eden of their youth, indulging in one of the earliest recorded intellectual exercises, that of giving names to things? Classification is but an attempt towards that order without which there cannot be progress.

The earliest classifications on record have for the most part a utilitarian basis—distinguishing the edible and the nauseous, the useful and the harmful, and so on, in which there is the salt of common sense and the warrant of indisputable utility. Whatever merits the modern classification of snakes may lay claim to, it can hardly dispense with the primeval distinction between the venomous and the innocent.

Early Classifications.

But man cannot be utilitarian always, and classification became physiological. Animals were grouped

according to their habits—fish of the sea, birds of the air, beasts of the earth, and things under the earth; as carnivores, herbivores, and omnivores; and it is not very long since even expert ornithologists classified birds as waders and divers, climbers and scratchers, and so on. This mode of classification is always as interesting as it is natural, but its value is discounted by the fact that similarity of habit or habitat does not necessarily imply natural affinity. Bats are not birds because they fly in the air, nor whales fishes because both live in the sea.

Physiological Classification.

The first great step to a more technical, and therefore truer, classification was made by Aristotle (384–322 B.C.), for his grouping was based on similarities of structure. Although he did not tabulate a classification as such, he was the first to draw that useful, but now somewhat hazy, line between the backboned and the backboneless, between the "lower" and "higher" animals. Thanks in part to the specimens which his pupil Alexander sent him, he knew about 500 different animals—far more, if one pauses to count, than most of us can even name, and, although he made the mistake of regarding the backboneless animals as *bloodless*, his classification reveals the insight of the true taxonomist.

Aristotle.

Aristotle's outline remained practically unaltered for eighteen centuries, the first to modify it to any purpose being Wotton (1492–1555), a London physician, who published a work, *De Differentiis Animalium*, in 1552, and introduced a large but heterogeneous group of zoophytes. The encyclopædists, such as Gesner, Johnstone, and Aldrovandi, added considerably to the list of known forms, but made no improvements of moment in their classification. Of importance, however, was the work of John Ray (1628–1705), the worthy predecessor of Linnæus. He was the first to define the use of the term "species", and to lay emphasis on anatomical characteristics as a basis of classification. For these reasons he may, as Professor Ray Lankester observes, be considered "the father of modern zoology".

Ray and Linnæus.

Following on the steps of Ray, Linnæus (1707–1778) established the binomial system of nomenclature, and the grades of classification (class, order, genus, species, variety). His great work, the *Systema Naturæ*, which forms the starting-point of modern taxonomy, passed through twelve editions in the course of his lifetime. (12th ed. 1768).

Lamarck.

The rapid progress of anatomy, now rendered more precise by the example of Linnæus, led to a multiplication in the number of classes. Linnæus had recognized six — Mammals, Birds, Amphibians (including Reptiles), Fishes, Insecta, and Vermes; it was one of Lamarck's achievements to do something towards the setting the great lumber-room of "Vermes" in order. He established sixteen classes instead of six, and his list of genera was ten times longer than that of Linnæus. His classification (1801–1812) represents the climax of the attempt to arrange the groups of animals in linear order from lower to higher, in what was called a *scala naturæ*.

We may trace to Cuvier four distinct contributions to classification:—

Cuvier.

(1) More than the best of his predecessors he placed classification on an anatomical basis. This is a sure foundation in proportion as the anatomy is accurate and thorough, which could not always be said even of Cuvier's. Thus in his *Règne Animal* (Paris, 1829) the barnacles are still among Molluscs, and the Batrachians among Reptiles.

(2) He opposed the erroneous conception of a *scala naturæ*, and sought to establish the idea of diverging branches or "*embranchements*", the beginning of what we would now call a genealogical tree. The branches he recognized — Vertebrata, Mollusca, Articulata, and Radiata—were indeed too few, and only the first remains now in the minds of zoologists very much as Cuvier saw it, but his leading idea of divergent lines represents a great step in classification. It must be remembered, however, that these lines did not mean to Cuvier, as they might have meant to his contemporary Lamarck, lines of evolution. The idea in Cuvier's mind was quite static.

(3) In founding palæontology, Cuvier did a twofold service to classification. He showed that the extinct forms were just as much subjects of scientific inquiry as the living forms; he also showed that just as the anatomy of recent animals aided in a

reconstruction of the fossil fragments, so the recognition of extinct forms aided in the arrangement of their living successors, filling up some of the morphological gaps.

(4) The work of Cuvier must always be associated with the idea of the "correlation of parts"—that the organism is a morphological unity. Certain characters are invariably correlated, others as invariably exclude one another; in short, the part is of a piece with the whole.

Recognition of the Embryological Basis.

The anatomical and palæontological foundations of classification were recognized by Cuvier, but there is a third foundation, namely in embryology. It seems fair to credit Von Baer (1792–1876) with laying this third foundation, not so much because he confirmed on embryological grounds the four *embranchements* of Cuvier—which was a mistake in detail—but because he saw clearly that the study of development was a sure clue to relationship. We find the same idea in the work of Johannes Müller (1801–1858), whose genius influenced almost every department of zoology; in Vaughan Thompson's discovery of the Crustacean nature of Barnacles; and conspicuously in Kowalewsky's account of the development of Ascidians and the lancelet (1866).

Genealogical Trees.

The pedigree of a noble stock, and the relationships between the different branches of the family, may be conveniently represented by a number of diverging and forking lines, and these may readily assume a more or less artistic tree-like arrangement, which has certainly the merit of vividness.

It is certain that, before the Theory of Descent was accepted or even discussed, genealogical trees were used to represent possible relationships among human races, or possible affinities among animals. It was used as a "graphic" way of expressing classification, and was true just in proportion as the classification was true. The naturalist-traveller Peter Pallas was one of the first to use it to express affinities among animals, though it is possible he saw a deeper meaning in his symbol.

But when the Theory of Descent took hold on men's minds, the genealogical tree became more than a graphic

register of affinities, it was used to express the supposed facts of descent. To Ernst Hæckel belongs the credit, or, as some critics would say, the responsibility of introducing the use of genealogical trees in zoology and botany. In his *Generelle Morphologie* (1866), and in his *Schöpfungsgeschichte* (9th edition, 1897), he displayed numerous genealogical trees designed to show the descent of various stocks and types of animals and plants.

There can be no doubt that in so doing he focussed the idea of descent into vividness, and by the very definiteness of the notation forced naturalists to a criticism of the reality of the supposed lines of descent.

Prof. L. von Graff says of Hæckel's *Stammbaüme*, "there is due to them the immortal credit of having given the first impetus to the grand revolution in the animal morphology of the last decades".

On the other hand, there are critics who maintain that the method is fallacious. If we had a knowledge of all forms that have lived, and a perfected classification of all these forms, then the tree-notation would be permissible. It would simply be another way of stating the perfected classification. But such perfection is unattainable. It is further urged, that while the notation may be permissible to express degrees of affinity, it has led by its symbolic suggestiveness to the common error of regarding a series of affinities as necessarily representing the actual line of descent. To take an obvious case, the double-breathing mud-fishes or Dipnoi are in many ways intermediate between fishes and amphibians, and might be appropriately represented in this position on a genealogical tree, yet it would be a mistake to suppose that the Dipnoi were the real ancestors of the Amphibia. But we cannot abandon a vivid notation simply because the careless read more into it than it is meant to express.

In justice to Hæckel, a single sentence may be quoted:—"Of course this genealogical tree, which represents the natural classification (system) of organisms, can never be drawn with absolute certainty, but always only in approximation thereto".

At the present day, though the origins of many of the great branches seem more uncertain than ever, some of the minor ramifications are being worked out with what seems strong probability of accuracy. In course of time it may be possible to piece the smaller branches together after the fashion of a puzzle picture.

Grades of Classification.

Before the work of Ray, the term "species" was used quite loosely, as it still is by the careless conversationalist who speaks indifferently of "the fish species" or "the human species". According to Ray, however, all similar individuals which exhibited constant characters from generation to generation form a species, and should be called by a particular name. Thus there is in Britain one species of daisy, but there are several species of buttercups. At the same time, Ray observed that the two sexes of the same species might be very different, and that one species of plant might "*degenerate*" into another.

Linnæus defined species as Ray had done, but even more rigidly. Each species was descended, he said, from an originally created pair, and each expressed an idea in the divine mind. Moreover, these ideas were consecutive, each species being intermediate between two others in the great system of nature, wherein, as Leibnitz had insisted, there was no leap or hiatus. Thus two long-lived dogmas were formulated: (*a*) the fixity of species, and (*b*) the doctrine of continuity—*natura non facit saltum*. At present no naturalist accepts the first, and many are very doubtful about the second.

To each species, as we have already noted, Linnæus gave a double name; thus the lion was called *Felis leo* and the daisy *Bellis perennis*, the second name being the specific title, while the first name was that of the genus—a group of more or less similar species. Similarly, Linnæus grouped genera into orders, and orders into classes.

No great change has been made in the grades of classification. In 1780 Batsch introduced the useful grade "family" between the order and the genus; Hæckel introduced (1866) the term "phylum" for any distinct branch of the genealogical tree, whether it in-

cludes one class or several; and Lankester introduced (1877) the terms "grade" and "sub-grade" for even larger divisions; thus:—

Grade B. Metazoa (multicellular)	Sub-grade Cœlomata (with body cavity). Sub-grade Cœlentera (without body cavity).
Grade A. Protozoa (unicellular)	Sub-grade Corticata (with cortex). Sub-grade Gymnomyxa (naked).

Conception of Species.

According to Linnæus, the individuals composing a species were all descended from an originally created pair, whose characters had persisted and would continue to persist as they were at the first. The number of species might diminish in the course of nature, but it could not increase apart from creation. "There are as many species", he said, "as issued in pairs from the Creator's hands." "There are just so many species as in the beginning the Infinite Being created." Apart from the outcrop of evolutionist views, which were but little heeded, this view of species remained dominant until 1859, when it found its most elaborate expression in L. Agassiz's *Essay on Classification*, and its death-blow in Darwin's *Origin of Species.* While workers like Cuvier had given quite objective definitions, "A species is an assemblage of individuals born by the same parents and of those which resemble these as much as they resemble one another", Agassiz regarded each species as the expression of a divine idea, fixed and eternal. "A species", he said when once asked, "a species is a thought of the Creator." So engrained are evolutionary ideas in the mind of the modern student that he finds it difficult even to understand the famous essay of Agassiz, especially when the author proceeds to regard even genera, orders, and classes as created. "This climax", Prof. Ray Lankester notes, "was reached at the very moment when Darwin was publishing the *Origin of Species*, by which universal opinion has been brought to the position that species, as well as genera, orders, and classes, are the subjective expressions of a vast ramifying pedigree in which the only objective existences are individuals, the apparent

species as well as higher groups being marked out, not by any distributive law, but by the purely non-significant operation of human experience, which cannot transcend the results of death and decay."

To the very last Louis Agassiz maintained his conviction that "there is no evidence of a direct descent of later from earlier species in the geological succession of animals"; and the famous *Essay on Classification* appears throughout to involve a misunderstanding of what classification really is. At the same time, it must be remembered that this great naturalist saw clearly that the various forms of life are not chaotic, that they can be put in order, that there *is* a *Systema Naturæ*, and a progressive development which he chose to express only in transcendental terms.

The modern conception of species may be expressed as follows:—When we see individual organisms very like one another, and so well marked off from their nearest neighbours that it is possible to distinguish them, we find it convenient to give them a specific name. Before doing so, if there is opportunity, we take certain common-sense precautions. We inquire whether the distinguishing marks which have arrested our attention have any real constancy, whether they persist through successive generations. What is more difficult is, to distinguish acquired characters or modifications, which are assumed by each individual in its lifetime as the result of external conditions, from inborn characters which form the real basis of the specific inheritance. We also inquire whether the distinctive characteristics in question are greater than those variations which are so often exhibited among the progeny of a single pair. Thus, no one would propose to divide men into species according to the colour of their hair or eyes, since that would land one in the absurdity of placing two brothers in different species. We also find out whether the members of the proposed species are fertile *inter se*, and tend to be sterile when crossed with the members of a related species.

To sum up, a species is a relative conception, convenient when we wish to include under one title all the

members of a group of individuals who resemble one another in certain characters. There is no absolute constancy in these specific characters, and one species often melts into another, with which it is connected by intermediate varieties. At the same time, the characters on account of which the naturalist gives a specific name to a group of individuals, should be greater than those which distinguish the members of any one family, should show a relative constancy from generation to generation, and should be associated with reproductive peculiarities which tend to restrict the range of mutual fertility to the members of the proposed species.

The invaluable order and precision introduced by Ray and Linnæus involved an exaggeration of the constancy and the discontinuity of species,—an exaggeration which evolutionary systematists have been slowly endeavouring to correct.

Chapter III.

Classification of Plants.

Ancient Classification—Mediæval Mysticism—The Herbalists—Cesalpino—Linnæus—Development of the Natural System.

The history of the successive attempts to classify plants is not readily condensed; it occupies over two hundred pages in Sachs's *History of Botany*, where no words are wasted. Some condensed summary must, however, be attempted, for it is impossible to appreciate the present position without going back to the Jussieus, and the Jussieus force us back to Linnæus, and Linnæus back again to Cesalpino.

Ancient Classification.

The ancient classifications were childish in outline and utilitarian in detail. "Herbs, shrubs, and trees"—these three words for many centuries formed the outline of the classification; the details referred to the diseases which the plants were believed to cure. We need hardly say more in

regard to the botanical contributions which the curious may unearth from the works of Aristotle, Theophrastus, Dioscorides, Pliny, and Galen.

Mediæval Mysticism.

The textual obscurities of the works inherited from the ancients involved a loss of time and energy quite out of proportion to the whole value of the legacy. Instead of observing or experimenting, the inquirer wasted his ingenuity in trying to find out what the ill-described plant could be which Dioscorides had credited with so many virtues. Moreover, the minds of most inquirers were filled with that interesting but lamentable mysticism, which saw nature as magical and symbolic instead of real and rational, and found expression in the long-lived doctrine of "signatures". According to this superstition the shape of a leaf, the colour of a flower, or the like, was a sign of the use for which the plant was meant.

The Herbalists.

The scientific renascence of the sixteenth century, which sent throbs of new life in so many directions, touched even the systematic botanist, and we find a succession of herbalists who looked out with fresh eyes upon nature, describing and drawing with loving care. Even their names are now unfamiliar—Brunfels, Fuchs, Bock, Dodoens, De l'Ecluse, De l'Obel, and Bauhin—save perhaps when one wonders for a minute over the commemorative name of some plant, like Lobelia or Bauhinia. But they mark an important transition from traditional to real botany, and it is with their painstaking enthusiasm that we associate the beginnings of precise descriptions, careful drawings and engravings, herbaria, local "floras", botanical excursions, and even gardens. The greatest of them, after whom came a decline, was Kaspar Bauhin (1550–1624). In his hands descriptions rose to the dignity of terse diagnoses, and he preceded Linnæus in giving each plant at least two names. Like the other herbalists he was weak in his general classification, but full of insight in his minor groupings, sometimes reaching, as if by a sort of insight (the subconscious result of very thorough description), to a recognition of natural affinities.

While the herbalists were working away with quiet enthusiasm in the north, and before their labours reached their culmination in the industry of Bauhin, a greater than any of them had arisen in the south. This was Andrea Cesalpino (1519–1603), a "thinker in presence of the plant world". Although he was Aristotelian in bone and marrow—a teleologist, that is to say, and a believer in "the vegetable soul"—he displayed an intensity of observation which was new, and he originated a mode of classification which, though eventually proved to be erroneous, was none the less fruitful. Although he denied the sexuality of plants, and had no idea of the real functions of leaves, he laid the foundations of comparative morphology, and elaborated a classification—an artificial classification—based on characters of seed, fruit, and flower. He seized upon certain characteristics—all too partially conceived—and forced plants into his *a priori* scheme, with the result that not more than three of his fifteen classes bear any approximation to natural groups. Had the lesson of his failure been rightly read, more than two centuries of taxonomic labour might have been saved.

Cesalpino.

To the careless and non-evolutionist readers of the history of botany Linnæus (1707–1778) was a sudden emergence, a discontinuous variation, a revolutionist who introduced order. But the facts point to a different interpretation; he was a synthetic genius who gathered up what was best in the work of the systematists from Cesalpino to Tournefort, and made a better of it. This is no depreciation; it is true even in regard to Darwinism; Linnæus was one of the "great men" in the history of science, but no small part of the secret of his greatness lay in the fact that he appreciated the work of his predecessors. The period from Cesalpino to Linnæus included a succession of illustrious workers, of whom the most important were Joachim Jung (1587–1657), Robert Morison (1620–1683), John Ray (1628–1705), Bachmann (1657–1725), and Tournefort (1656–1708).

Linnæus.

Linnæus was pre-eminently a describer and system-

atist; as Sachs puts it, "he might almost be said to have been a classifying, co-ordinating, and subordinating machine". His physiology was not even up-to-date; of pedigrees he had at most a fleeting idea. His main desire was to name and to arrange, and in this he did service by emphasizing the importance of the stamens, which served him better than he had—from our point of view—any right to expect.

He classified flowering plants with especial reference to the number of the stamens, as Monandria, Diandria, Triandria, &c.; and this narrow basis often led him to right results in the detection of affinities. It is a remarkable fact in the history of classification that characters which at first sight do not seem to be of great importance, may nevertheless serve as good indices to affinities.

Though it was, in a sense, only a scientific trick, the establishment of the binomial nomenclature, by which each kind of organism received two names, a generic and a specific, *e.g.* *Bellis perennis* (the daisy) or *Viola canina* (the dog violet), has proved of great service in classification, and although it cannot be called the invention of Linnæus, it was certainly established by him.

In the eyes of his contemporaries the great service of Linnæus was that he established greater order than heretofore in the maze of living forms. In the eyes of his modern successors "the greatest and most lasting service which Linnæus rendered both to botany and zoology lies in the certainty and precision which he introduced into the art of describing".

For the order which he established was, on the whole, an artificial order, corresponding to nothing real in the genetic relationships of plants. At the same time, it must be remembered that Linnæus had an esoteric classification, as it were, a sketch of a *natural system* (a true *systema naturæ*), the merits of which were duly recognized by the Jussieus (uncle and nephew), who laid the foundations of our modern arrangement of flowering plants.

While many of Linné's successors seem simply to

have vied with one another as to the number of plants which they could name, and the precision—often becoming preciosity—with which they could describe them, a qualitative advance towards a natural system of classification was made by others who discerned and developed the more esoteric doctrines of their master. The establishment of a classification based on genuine structural resemblances was the outcome of the labours of a long succession of workers from the Jussieus, Joseph Gärtner, Auguste Pyrame de Candolle, and Robert Brown, to Endlicher and Lindley, and the systematists of to-day. For more than a hundred years after Linnæus, the classification slowly grew in stability and reality, but quite unillumined by any thought of evolution. It was helped by the study of development, and by the increased precision of anatomical analysis, but it remained strictly Linnæan in one sense at least—that it was dominated by the dogma of the constancy of species.

Development of the Natural System.

Bernard de Jussieu (1699–1777), memorable to the zoologist for having, along with Peissonel, first denounced the prevalent view that corals were plants, laid out the beds in the royal garden of Trianon, so as to express his views on the natural affinities of the orders. These views were based on Linné's fragment of a natural system, and they doubtless led on to his nephew's much stronger work.

Antoine Laurent de Jussieu (1748–1836) is forever memorable for his *Genera Plantarum* (1789), the main feature of which was the characterization of the *families* of plants. As Sachs says, Bauhin gave characters to species, Tournefort defined genera, Linnæus grouped genera, the younger Jussieu diagnosed families. In other words, he effected an induction of a higher order of complexity than those which his predecessors had achieved.

Joseph Gärtner (1732–1791) did service to natural classification by his monograph on fruits and seeds, which Jussieu and a few others were able to appreciate. He was one of those remarkable men whose records

astound the modern specialist. We hear of him as a student of zoology and of physics, as a professor of anatomy in Tübingen, and of botany in St. Petersburg; yet, Sachs says, "he gives us the impression of a modern man of science more than any other botanist of the eighteenth century, with the exception of Koelreuter".

To Auguste Pyrame de Candolle (1778–1841) may perhaps be given the palm of maximum productivity among botanists, and that is saying much. He experimented, herborized, travelled, monographed, and pondered, producing an amount of botanical work which has been referred to by many as "incredible", and filled up his spare time with political and civic activities. His name is particularly associated with the famous *Prodromus Systematis Naturalis*, "the grandest work of descriptive botany that is as yet in existence". He had in a high degree what may be called "morphological insight", and moved through the mazes of classification with a much firmer step than any of his predecessors. In the emphasis with which he indicated the distinction between morphological and physiological characters, we may compare him, among zoologists, to Owen.

De Candolle's most illustrious botanical contemporary was Robert Brown (1773–1858), whom Humboldt called "botanicorum facile princeps". His first great achievement was bringing back from Australia a collection of about 4000 plants, in great part new species. His life-work was a series of monographs, which he leavened with the ideas of morphology. "The peculiar character of the natural system as compared with every artificial arrangement is brought out into higher relief by Robert Brown than by Jussieu and De Candolle, and he succeeded better than any of his predecessors in separating purely morphological and systematically valuable relations of organization from the physiological adaptations of organs." To Robert Brown also belongs the credit of emphasizing and utilizing the embryological basis of classification. In this he may be compared with Von Baer.

Systems of classification proposed by those who followed more or less faithfully the models of work furnished by De Candolle and Robert Brown grew and multiplied exceedingly; for many years in succession there was one of some pretensions each spring; the most noteworthy were those of Bartling, Endlicher, Brongniart, and Lindley, which bring us down to the time when evolutionary ideas began to assert their ferment-like influence.

It is not possible for us within our limits to follow the modern progress of systematic botany. The gist of a physiological discovery may often be stated briefly, but discoveries in classification require much exposition. That there has been great progress is certain. As Professor Marshall Ward has said, "The competent historian of our branch of science will have no lack of materials when he comes to review the progress of botany during the latter half of the Victorian reign. The task of doing justice to the work in phanerogamic botany alone, under the leadership of men like Hooker, Asa Gray, Mueller, Engler, Warming, and the army of systematists so busily shifting the frontiers of the various natural groups of flowering plants, will need able hands for satisfactory treatment. A mere sketch of the influence of Kew, the principal centre of systematic botany, and of the active contingents of Indian and colonial botanists working under its inspiration, will alone require an important chapter, and it will need full knowledge and a wide vision to avoid inadequacy of treatment of its powerful stimulus on all departments of post-Darwinian botany."

Chapter IV.

Study of Structure (Animal Morphology).

The Scope of Morphology—Foundations laid by Aristotle—Rise of Comparative Anatomy—Cuvier and Correlation—Cuvier's Contemporaries—Richard Owen—Huxley—Hæckel—Gegenbaur—Criteria of Homology—Physiological Morphology.

The term morphology, introduced by Goethe, is here used in its widest sense, to designate the science of organic form and structure. As Geddes puts it, morphology is the study of the organism in its *static* relations, while physiology is the study of the organism in its *kinetic* relations. At different levels of analysis morphology seeks an answer to the question, "*What is this in itself and in its parts?*" It includes anatomy and histology, not only of the adult, but of the young and embryonic stages, and not only of modern forms, but of extinct types as well. And although we have, for convenience sake, discussed classification or taxonomy separately, this is also part of morphology, one of the main aims of which is to detect structural affinities, now known to express genetic relationship.

The Scope of Morphology.

As in many other departments, the work of Aristotle is fundamental in morphology. He knew about five hundred different animals, he studied the internal structure of a few, and he suggested the first scientific classification. It is true that he failed to discriminate between nerves and tendons, or to understand what either brain or muscles meant, but he approached some of the great generalizations of morphology, such as the correlation of organs and the conception of homology. The remarkable historical fact has already been noted, that apart from the works of Galen (born A.D. 130), who made some anatomical researches on Mammals, the foundations laid so securely by Aristotle remained practically unbuilt upon until the sixteenth century.

Foundations laid by Aristotle

Galen had only been permitted to dissect monkeys, and human anatomy was largely conjectural until Vesalius placed it on a sure basis in the sixteenth century. This was not only important in itself, but it raised a standard of accuracy which gave a stimulus to the zoological anatomist—a stimulus which has often been repeated in the history of the science. Many zoologists have acknowledged their indebtedness to their discipline in human anatomy.

Rise of Comparative Anatomy.

In the encyclopædic period anatomical researches began to become common, monographs on different groups were published, and huge treatises, like Gesner's *Historia Animalium* (1551–1558), with 4500 folio pages, made their appearance. In these, however, there seems to have been rarely any deep morphological note; there was dissection but without comparison, analysis but without synthesis. In Belon's *Birds* (1555) there is "a comparison of the skeletons of Bird and Man in the same posture, and as nearly as possible bone for bone"; and in 1645 Severinus published his *Zootomia Democritæa*, "the first book devoted exclusively to the general subject of comparative anatomy".

In the seventeenth century Harvey discovered the circulation of the blood (1616, announced 1628), and carefully dissected the heart; some of the early microscopists, *e.g.* Malpighi and Swammerdam, turned their attention to the structure of the lower animals; and the progress of classification in the hands of Ray and Linnæus reacted on anatomy.

In the eighteenth century there were some great workers more or less on comparative lines. John Hunter dissected and observed with untiring industry, and Vicq d'Azyr struck an even clearer morphological note.

Cuvier and Correlation.

Georges Cuvier (1769–1832) was not only great in himself and his work, but in his school, for he dominated most of the zoological work of the first half of the nineteenth century. He dissected many animals which had not previously been touched; he insisted on the anatomical basis of classification; and he recognized that there were several divergent types of structural architecture (Vertebrate, Molluscan,

Articulate, and Radiate); but perhaps his greatest contribution to morphology was his conception of the correlation of parts.

This fruitful idea is the morphological aspect of the unity of the organism. It suggests that an organism is not a hap-hazard aggregate of characters, but a unified integrate. Part is bound to part, so that if the one varies the other varies with it. In short, "there are many members which are members one of another, in one body". An animal with a cud-chewing habit or ruminant stomach has always "a cloven hoof"; the presence of gills implies the absence of the fœtal membrane known as the allantois. To Cuvier's mind the "correlation of parts" was simply a morphological fact; to us it suggests two ideas: that related forms have sprung from a common stock, and that the characters of each organism are unified in some unknown way in the constitution of the fertilized ovum, and in the progress of its development.

There is no doubt, moreover, that Cuvier exaggerated the truth of his guiding principle. In his famous *Discourse on the Revolutions of the Surface of the Globe* (1812–1813) he says, "a claw, a shoulder-blade, a condyle, a leg or arm bone, or any other bone separately considered, enables us to discover the description of teeth to which they have belonged; so also, reciprocally, we may determine the form of the other bones from the teeth. Thus, commencing our investigation by a careful survey of any one bone by itself, a person who is sufficiently master of the laws of organic structure may, as it were, reconstruct the whole animal to which that bone had belonged." There is no living morphologist who would accept so exaggerated a statement.

Cuvier's Contemporaries.

To understand Cuvier's stern opposition to theoretical speculation, and his insistence on the fundamental importance of anatomical analysis, we must remember the saturating influence of the "*Naturphilosophie*" of Schelling and his school, with all its vague ideas as to the unity of nature and Platonic archetypes. With this transcendental

anatomy, useful as it often was in stimulating both research and thought, Cuvier had no sympathy. This should be borne in mind when we consider his antagonistic attitude to men like Lamarck, Etienne Geoffroy St. Hilaire, and Goethe.

Diverse opinions are held as to the value of Goethe's morphological work, but, as Geddes says, "that he discerned and proclaimed, and that more clearly than any of his predecessors or contemporaries, the fundamental idea of all morphology—the unity which underlies the multifarious varieties of organic form,—and that he systematically applied this idea to the interpretation of the most important, most complex, and most varied animal and vegetable structures is unquestionable". "Independently of Vicq d'Azyr, he discovered the human premaxillary bone; independently of Oken, he proposed the vertebral theory of the skull; and before Savigny, he discerned that the jaws of insects were the limbs of the head."

Of greater influence than Goethe, however, was Etienne Geoffroy St. Hilaire, author of the *Philosophie Anatomique* (1818–1823), who elaborated and exaggerated the doctrine of unity of type. Tainted by the transcendentalism of the *Naturphilosophie*, he is perhaps more memorable for his intentions than for his achievements, but he was the first expert comparative anatomist who was at the same time an evolutionist. In his controversy with Cuvier before the Academy of Sciences in Paris (1830), as to the unity of structure which he supposed to obtain between cuttle-fishes and vertebrates, he was utterly defeated; but the defeat, as subsequent progress soon showed, was rather as to the letter than as to the spirit.

Richard Owen.

Owen (1804–1892) links Cuvier to Huxley and Gegenbaur, occupying a strange midway position; on the one hand, extremely conservative and unappreciative of Darwinism; on the other hand, really believing in the derivation of species from one another.

Beginning with the monumental *Descriptive and Illustrated Catalogue of the Physiological Series of Compara-*

tive Anatomy (1833–1840), founded upon John Hunter's preparations, Owen may be said to have spent much of his life in expanding it. From orang to duckmole, from pearly nautilus to Venus's flower-basket, a long series of interesting types yielded many of their secrets to his anatomical skill. In 1866–1868 he summed up many of his results in his *Anatomy and Physiology of the Vertebrates*, which Sir William Flower, who has developed the British Museum of Natural History far beyond Owen's dreams, calls "the most encyclopædic work on the subject accomplished by any one individual since Cuvier's *Leçons d'Anatomie Comparée*".

Minute studies of the skeletons of living animals, and of their teeth in particular (*Odontography*, 1840–1845), enabled Owen, like his master Cuvier, to win great success in the reconstruction of the extinct. His memoirs on the gigantic sloth *Mylodon*, on the giant birds of New Zealand, on *Archæopteryx*, the oldest known bird, on the extinct reptiles of Britain, on the fossil Belemnites from the Oxford clay, remain, along with many others, well-known classics.

Owen excelled Cuvier in the accuracy of his work and in the generalizing spirit which he brought to bear upon his problems. The working out of the structural contrasts between even-toed and odd-toed hoofed mammals (Artiodactyl and Perissodactyl Ungulates) may perhaps be cited as representative of his best morphological work, while his persistent adherence to the vertebral theory of the skull (which interprets the skull as composed of a few segments each comparable to a vertebra) illustrates his worst. It was characteristic of him to go doggedly along his own path with scant attention to what others were achieving. In another respect, his work seems disappointing, though it is perhaps difficult, in our modern atmosphere, to judge justly on the matter; we refer to his attitude to evolution doctrine. It is certain that he was no supporter of the "special creation" hypothesis, but his utterances suggest half-heartedness as regards the theory of evolution. One of the most explicit reads: "So, being unable to accept the volitional hypothesis, or that of impulse from within, or

the selective force exerted by outward circumstances, I deem an innate tendency to deviate from parental type, operating through periods of adequate duration, to be the most probable nature, or way of operation, of the secondary law, whereby species have been derived one from another".

Apart from the results of anatomical analysis, though really inseparable from these, the greatest service which Owen rendered to the science of morphology was his clear definition of *homology* and *analogy* (1843), the former being illustrated by "the same organ in different animals under every variety of form and function" (*e.g.* fore-limbs of *Draco volans* and wings of Bird); the latter being illustrated by "a part or organ in one animal which has the same function as another part or organ in a different animal" (*e.g.* parachute of *Draco* and wings of Bird). In other words, organs of similar function are analogous, organs of similar structure and development are homologous.

The conception of homology was worked out in greater detail by Owen, but we cannot discuss it, nor its further elaborations by Agassiz and Bronn, Hæckel and Mivart. The most important modification is due to Lankester, who, in 1870, distinguished *homogeny*, or correspondence due to common descent, from *homoplasty*, "that close agreement in *form* which may be attained in the course of evolutional changes by organs or parts in two animals which have been subjected to similar moulding conditions of the environment, but have no genetic community of origin to account for their close similarity in form and structure".

Huxley.

Although we rank Huxley (1825–1895) among the morphologists, it was not in this capacity that he left his deepest mark on British biology. For his influence mainly depended on the fact that he combined in extraordinarily high development the scientific and the practical mood. In illustration of Huxley's scientific mood we may refer to the high ideal of accuracy which characterized his work and writings, and quite as markedly his popular lectures, to the caution which made him so reserved as to any causal theory of

evolution, to the power of perceiving wide relations, which enabled him to place almost every subject he touched in a new light and larger perspective, to the critical Cartesian spirit which made him at an early date keenly aware of the limitations of widely accepted generalizations, such as the Cell-Theory, the Recapitulation Doctrine, or the utility of all organic characters.

Of Huxley's practical mood illustrations abound. He entirely changed the character of biological teaching, and was one of those who did great service many years ago by insisting on practical work as an essential part of discipline in natural science; he wrote model text-books, *e.g. Lessons in Elementary Physiology* (1866), and he brought science within reach of the people perhaps more effectively than any other has ever done. On the Fisheries Commission, on the London School Board, as the preacher of "Lay Sermons", as the champion of free thought and free speech, and as the restless critic of current movements in politics and social science, he was intensely practical, and one of the last efforts of his life was the Romanes lecture on "Evolution and Ethics". To him science was for life, not life for science.

What we have said above seems to explain what has been often noticed in regard to Huxley, that, although an inspiring teacher, he founded no school; that, although the cutting-edge of evolution doctrine, he added nothing directly to its content; that, although most keenly interested in physiology, he made no physiological discoveries; that, although he systematized the teaching of biology, he added very little to its capital of ideas. It is easy to say, that, if he had worked less for fisheries, he might have worked more at fishes; if he had paid less heed to the bishops, he might have done more for biology; but such reflections are gratuitous. In Huxley the scientific and the practical mood were both very strongly developed, and his life was the natural expression of this.

Of Huxley's masterly way of dealing with facts, the non-biological reader may gain an impression from his lectures and essays which have been republished in nine volumes, from his articles "Biology" and "Evolution"

in the *Encyclopædia Britannica*, from the introduction to his *Anatomy of the Invertebrates* (1870), from the introduction to zoology, entitled *The Crayfish* (1881), from *Man's Place in Nature* (1863), and *American Addresses* (1879).

His more technical scientific memoirs are being republished under the editorship of Profs. Michael Foster and E. Ray Lankester, and among the most important may be noticed those which discuss the anatomy and affinities of the Medusæ (1849) (whence sprang the generalization that the embryonic epiblast and hypoblast correspond to the two layers of a polype's body), the fossil ganoids, the vertebrate skull (including an anatomical demolition of the vertebral theory which lasted from Oken to Owen), the classification of birds (based on the skeletal features of the skull), the union of birds and reptiles in the major group Sauropsida, and of amphibians and fishes in the major group Ichthyopsida.

Hæckel.

Two great biological books were completed in 1866, Mr. Herbert Spencer's *Principles of Biology* and Prof. Ernst Hæckel's *Generelle Morphologie*; and though they are very different in mood and style, they have the common aim of presenting an ordered system of biological generalities. In the *Generelle Morphologie*, we find long discussions on the forms assumed by organic structures and by entire organisms, a subject ("promorphology") to which little attention has been paid since; on the theory and grades of individuality—both physiological and morphological, a subject which was pursued by many till all biologists wearied of it; on the categories of homology and the principles of classification; on the different modes of reproduction; on heredity and evolution. Like its English analogue mentioned above, it presented not only a critical account of the general conclusions which had been reached, but a further development of each, and an orderly arrangement of the whole. To those who seek for a survey of the whole field in the perspective of 1866, which has not been essentially changed since, the two works are invaluable, as also to those who fancy that they have new ideas on the subject.

Gegenbaur.

As the author of the most impressive text-book, *Elements of Comparative Anatomy*, which has appeared since Huxley's, Prof. Carl Gegenbaur is well known to all students of zoology. A fellow-student of Hæckel's, he expresses in his work a combination of the methods of comparative anatomy and embryology under the dominance of evolutionary ideas.

Gegenbaur's detailed work is all of importance, but it cannot be summarized here. A single illustration must suffice, concerning a problem with which his name is specially connected—the theory of the vertebrate head. This is "the most complex piece of animal architecture with which anatomists have to deal", and there has been a long-standing question as to its structural plan. In 1806, Oken stumbled on the first solution. As he was walking in the Harz Forest, he found the blanched skull of a sheep; he picked it up, and remarked, "It is a vertebral column". This remark was the first expression of his "vertebral theory", which resolved the skull into three parts comparable to vertebræ. This theory was afterwards claimed by Goethe, who may have reached it independently or by unconscious assimilation, and it was afterwards widely accepted and championed by such an authority as Owen. In 1869, Huxley attacked the problem, and showed that the vertebral theory was anatomically fallacious. He showed, for instance, that when attention was directed to the cranial nerves and the gill-slits, a large number of head-segments were recognizable. Two years later (1871), Gegenbaur took up the subject on a broader embryological basis, and between the two great workers the "vertebral theory of the skull" ceased from troubling. Like many another dream of the "Naturphilosophie" school, it vanished when brought into touch with facts. Gegenbaur showed that the tenth or vagus nerve, which is distributed to several gill-clefts, must be regarded as composite and corresponds to at least four segments; that in the lowest (gristly) fishes, where hints of the original vertebræ might be most expected, the skull is an unsegmented gristly brain-box; and that in higher forms the vertebral nature of the skull cannot

be thought of for a moment, since many of the bones (*e.g.* along the top of the skull) arise in the skin.

Gegenbaur has been a powerful exponent of the idea that new structures do not arise *de novo*, but from alterations in pre-existing structures. Thus he has been a supporter of the theory that the limbs of vertebrates have arisen from an alteration in the position and function of some of the branchial or visceral arches whose original use was to support gills.

As another instance we may refer to the musculature of the tongue. This does not occur in fishes, whose tongues are all non-muscular. The mobility begins in amphibians, and Gegenbaur has shown that the muscles are at first too small and weak to be used to move the member. They serve in the young tadpole merely to compress the glands of the tongue, but they grow in strength and take on a new function which has been of great importance to amphibians and higher animals.

The basis of a natural classification, and what comes to the same thing, a probable pedigree, has been found in the recognition of homologous structures in different organisms. It is therefore of great importance that the homologies be secure, and it is distinctive of modern morphology that the question of the criteria of homology is not treated in the easy-going fashion that was for a time prevalent.

Criteria of Homology.

Historically, the case stands thus. To Owen, homology meant anatomical correspondence in the relative position and connections of parts. Gradually the anatomical correspondence found embryological corroboration, and this was most welcome. But the modern enthusiasm for embryology and the influence of the Recapitulation Doctrine have led to a predominance of the embryological, and a partial superseding of the anatomical criteria. This has often given rise to a wildness of speculation as to pedigrees (phylogeny) which leaves the anatomist bewildered.

From this exaggerated confidence in the embryological revelation of relationships, the inevitable reaction has ensued. Thus Prof. E. B. Wilson gives many examples which show that "embryological de-

velopment does not in itself afford at present any absolute criterion whatever for the determination of homology". Similar structures arise in different ways: "The stomodæum of *Lopadorhynchus* (an annelid worm) is undoubtedly homologous with that of the earth-worm, though the one appears as a paired, the other as a single median structure. The ventral nerve-cord of *Polygordius* (a primitive annelid) is certainly homologous with that of the earth-worm, though the former appears as a median unpaired thickening of ectoderm, while the latter arises by the concrescence of two widely separated halves." There is an extraordinary contradiction between the bud-development and the ovum-development in Tunicates, though the same results may be reached by the two methods. In fact, though it is a hard saying, "homology is not established through precise equivalence of origin, nor is it excluded by total divergence".

Thus we understand the reaction to the standard of Owen, which defines homology in reference to the structure and structural relations of the developed organ. As Prof. Wilson says: "We must primarily take anatomy as the key to embryology, and not the reverse. Comparative anatomy, not comparative embryology, is the primary standard for the study of homologies, and hence of genealogical descent. . . . It is the prospective and not the retrospective aspect of development that is decisive."

Gegenbaur, although in great part an embryologist, has been a consistent upholder of the position that comparative anatomy furnishes the secure basis of homologies. Prof. E. B. Wilson translates the following passage, which expresses Prof. Gegenbaur's position:—

"If we are compelled to admit that kainogenetic characters are intermingled with palingenetic, then we cannot regard ontogeny as a pure source of evidence regarding phyletic relationships. Ontogeny, accordingly, becomes a field in which an active imagination may have full scope for its dangerous play, but in which positive results are by no means everywhere to be

obtained. To attain such results, the palingenetic and the kainogenetic phenomena must be sifted apart—an operation that requires more than one critical *granum salis*. On what ground shall this critique be based? Assuredly not by way of a *circulus vitiosus* on the ontogeny again; for if kainogenetic characters are present in one case, who will guarantee that a second case, used for a comparison with the first, does not likewise appear in a kainogenetic disguise? If it be once admitted that not everything in development is palingenetic, that not every ontogenetic fact can be accepted, so to speak, on its face value, it follows that nothing in ontogeny is immediately available for the critique of embryological development. This conclusion cannot be escaped. The necessary critique must be drawn from another source"—namely, the results of comparative anatomy.

In some cases, however, the embryological verdict is clear and unambiguous, and there can be little doubt that the whole embryological story will become significant, and reliably so, when the progress of physiological embryology has made it possible to give a real and not a fanciful content to the terms palingenetic and kainogenetic.

Physiological Morphology.

It is difficult to find a proper term for the distinctively modern movement which inquires into the nature of growth-conditions. The Germans, among whom it originated and has made most headway, call it *Entwicklungsmechanik* or developmental mechanics (in Kant's sense), but we are at present a far cry from any vital mechanics in the English sense. Perhaps, therefore, the term physiological morphology is preferable.

Dr. Wilhelm Roux, who has the credit of setting this new department of science upon its feet, defines "developmental mechanics", or "causal morphology", as "the doctrine of the causes of organic forms, and hence the doctrine of the causes of the origin, maintenance, and degeneration of these forms".

One of the earliest exponents of this point of view was Prof. W. His, whose thoughtful work *Unsere Kör-*

perform has influenced many. He distinguished two factors in development: (1) the law of growth, which depends upon the inherited potentialities of the germinal material; and (2) the conditions of development, such as amount and distribution of yolk, pressure of membranes, and surrounding medium. In terms of these he sought to explain the foldings, the ingrowths, the outgrowths, and other processes in development. Prof. A. Rauber developed similar ideas in his *Formbildung und Formstörung*, and it is interesting to notice how this anatomist has of recent years made a specialty of crystallization. Prof. Sachs, on the botanical side, was also keenly interested from an early date in the problems of causal morphology.

The fresh movement has not, as yet, led to the solution of any big problem, but it has been attended with much detailed success. Hertwig and Driesch, Herbst and Dreyer, Wilson and Loeb, have been prominent among the many workers. The gist of their method is by artificial *Formstörung* to get hold of clues which may aid in the understanding of normal *Formbildung*; and although there is much disagreement—naturally incident on a new departure—the work of the experimental school has impressed biologists with the hopefulness of looking for the immediate stimuli and essential conditions which determine each successive expression of the potentialities of the germ-plasm.

Chapter V.

Study of Structure (Vegetable Morphology).

Early Anticipations—Metamorphosis in Flowering Plants—Wolff—Goethe—Subsequent Development—Foundations of Exact Morphology—Comparative Embryology—Alternation of Generations—Study of Algæ, Fungi, and Lichens.

Although it is possible to find in the works of Aristotle and Theophrastus, and other ancient authorities, in-

teresting sentences which have a bearing on vegetable morphology, these were only guesses at truth, and must not be taken too seriously. Thus, to quote three examples given by Dr. Masters, Aristotle is reputed to have said, "As a general rule, a plant possesses potentially both root and stem in every part"; Theophrastus said, "Some organs exist only according to analogy, and others, though the same, yet exist in a different manner"; and Nicolas of Damascus ventured the hypothesis that "leaves are properly speaking fruits". But it would be absurd to see in the last sentence, for instance, any prevision of a modern theory, that the vegetative leaf is derived from a sporophyll. There was practically no vegetable morphology until we approach the time of Goethe, who was the first to use the word.

Early Anticipations.

In this chapter we propose to consider two of the greatest modern morphological achievements in botany—the doctrine of metamorphosis, and the recognition of alternation of generations.

For many years morphological inquiry centred around the word metamorphosis, which Goethe defined (1790) as "the operation by which one and the same organ assumes various forms".

Metamorphosis in Flowering Plants.

Unfortunately, however, the word was not always used in the same sense; thus Linnæus used it quite loosely, sometimes in reference to the changes observed in normal development; sometimes in reference to the observable changes which are seen, for instance, when a wild flower becomes "double" under cultivation; and sometimes in other ways. But the ambiguity of most importance is this: (*a*) some used the word with definite *material* content to describe structural changes now observable, or supposed to have been observable in the course of the ages, *e.g.* the change of a vegetative leaf into a flowering leaf, or *vice versa*; (*b*) others used the word with a merely *idealistic* meaning, being content with convincing themselves that vegetative leaves and floral parts could be related *in thought* as metamorphoses of the idea which the supposed "archetypal" plant expressed.

The two names most intimately associated with the doctrine of metamorphosis are those of the embryologist Wolff and the poet Goethe, who arrived at the same conclusion—the homology of appendicular organs—by very different paths; but it is important to notice that previous attempts had been made to discover connections between the various structures which spring from the axis of a flowering plant. Thus Cesalpino had called the corolla simply a leaf ("folium"); he and Malpighi had also regarded the cotyledons as leaves; and the keen-sighted Joachim Jung had analysed the plant-body into root and shoot, and the latter into stem and leaf. As Prof. Vines notes, Jung "revealed striking morphological insight", and "grasped the fundamental ideas of morphology", but his works, which were not published till after his death (*Isagoge Phytoscopica*, 1678, &c.), had almost no influence. Linnæus also had an idea of the equivalence of the appendicular structures, as suggested, for instance, in the aphorism *Principium florum et foliorum idem est.* He developed his views in two dissertations entitled *Prolepsis Plantarum* (1760 and 1763), but these were obscured by a minor physiological theory, according to which the flower was regarded as an anticipation (*prolepsis*) of several years' growth of vegetative shoots. He did, however, refer all the parts of the flower to leaves, arguing from the numerous transitions, both normal and pathological, that the parts must be homologous. Only homologous parts, he said, can thus change into one another; "the liver cannot become the heart, nor the heart the stomach". Wolff's *Theoria Generationis* was published the year before the first *Prolepsis* essay, but Linnæus had made similar suggestions in his *Systema Naturæ* (1735) and in his *Philosophia Botanica* (1751).

Wolff.

Caspar Friedrich Wolff, who is best known as the founder of the embryological doctrine of Epigenesis, was led to a study of the development of plants by a desire to test the theory which he had reached from a zoological basis. He investigated the leaf-bud of the cabbage, the flower-bud of the bean, and the like, and showed that the various

"appendicular organs", whether ordinary leaves or floral parts, have a similar mode of development at the growing point (*punctum vegetationis*) of the stem. It was thus *inductively* that he reached the following conclusion (1767): "In the entire plant, whose parts we wonder at as being, at the first glance, so extraordinarily diverse, I finally perceive, after mature consideration, and recognize nothing beyond leaves and stem (for the root may be regarded as a stem). Consequently all parts of the plant, except the stem, are modified leaves."

What is particularly significant in Wolff's work is that he sought in the study of development to find a secure basis for his theory that the parts of the flower are transformed leaves. "If", he said, "the organs of a plant, with the exception of the stalk, are thus referable to the leaf, and are mere modifications of it, a theory showing the manner in which plants are generated is obviously not a very difficult one to form, and at the same time the course is indicated which we must follow in propounding it. It must first be ascertained by observation in what way the ordinary leaves are formed, or in other words, how ordinary vegetation takes place, on what basis it rests, and by means of what powers it is brought into existence. Having gained this knowledge, we must investigate the causes which so modify the general mode of growth as to produce, in the place of leaves, the parts of the flower." His own peculiar theory was that the change from a foliar to a floral organ was due to a diminution of vegetative power (*vegetatio languescens*).

More than twenty years after Wolff, Goethe reached a similar conclusion on independent lines. One may

Goethe.

doubt the accuracy of his self-analysis when he said that he had been more influenced by Linnæus than by any one save Shakespeare and Spinoza, but it is certain that he was stimulated by the *Prolepsis*. For several years before he published his famous essay he was pondering over the problem of the flower, and it was doubtless this persistence "through long prosecuted studies" which enabled him to persuade himself that he had reached his conclusion inductively. The

story of his "painful surprise" when Schiller said, "This is not an observation, it is an idea", is interesting to the student of scientific method, the obvious fact being that Goethe reached his conclusion *deductively*, for his mind was full of the evolution idea, and that he tried to verify it *inductively*—a thoroughly sound procedure.

Goethe's theory of the morphological equivalence of appendicular organs was developed in his famous essay *Versuch die Metamorphose der Pflanzen zu erklären*, published in 1790. "In this brilliant essay", Prof. Geddes says, "the doctrine of the fundamental unity of floral and foliar organs is clearly enunciated, and supported by arguments from anatomy, development, and teratology. All the organs of a plant are thus modifications of one fundamental organ—the leaf, and all plants are in like manner to be viewed as modifications of a common type—the *Urpflanze*."

Prof. Vines points out that Goethe's evidence, if strictly considered, was by no means conclusive. He rested his case chiefly on the occurrence of transitional forms which connect different kinds of leaf-organs, and on monstrosities, such as stamens which become petals. But it is possible to find forms at least superficially transitional between leaf and shoot; and to argue from monstrosities is always precarious. The theory lacked, what Wolff had begun to supply, the "embryological criterion of homology". Moreover, as Goethe himself felt keenly, the theory remained vague and unsatisfactory in regard to *what it was* that had been the subject of all the supposed metamorphosis. "What he sought", Prof. Vines says, "was the morphological concept of the leaf; and the reason why he failed to form it was that the morphological botany of his time was too superficial and too physiological to admit of such conception." And as the observed facts of transitions and abnormal changes pointed to both ascending and descending metamorphosis, Goethe was puzzled, as many of us are still, as to the *direction* of the supposed evolution. Is it from vegetative leaf to floral leaf, or *vice versâ*? "For", as Goethe said, "we can as well

say a stamen is a contracted petal as we may say of the petal that it is an expanded stamen; or that a sepal is a contracted foliage-leaf, as that a foliage-leaf is an expanded sepal."

Subsequent Development.

The immediate successors of Goethe (for he had more influence than Wolff) were too much dominated by the mood and method of the "Naturphilosophie" to effect much progress. There was a plethora of speculation which often lost all touch with reality,—speculation as to "polarities" and "rejuvenescence", as to "the wave-pulse of metamorphosis" and "the spiral tendency of growth", and a host of similar verbalisms. As Prof. Vines says, the period "was fruitful in little else than wild theorizing", but it "fortunately culminated in a reaction to investigation and induction. On a sudden, as it were, a band of men arose, of brilliant ability and indefatigable industry, whose great achievements have revolutionized not only the department of morphology, but the other branches of botany as well; I need only mention the names of Schleiden, Von Mohl, Nägeli, Hofmeister, Robt. Brown, Irmisch, Hanstein, Alex. Braun." From these, through De Bary and Sachs, we pass naturally to Goebel and Bower, and other active morphologists of to-day.

In modern times the morphological equivalence of appendicular organs has been confirmed in three ways: (*a*) by careful observation of actual cases of transformation, *e.g.* of bud-scales; (*b*) by the microscopic investigation of apparently homologous parts; and (*c*) by more precise embryological evidence. There is no doubt that one kind of appendicular organ may be metamorphosed into another, or more generally, "that there is a genetic relation between the forms of the same member".

The direction in which the evolution has taken place —whether from foliage-leaf to reproductive-leaf or *vice versâ*—remains the subject of discussion. Goebel, for instance, strongly maintains the older view that the spore-bearing leaf (sporophyll) is a metamorphosed foliage-leaf, while Bower maintains that the foliage-leaf is a metamorphosed sporophyll, which has become

sterile. As Prof. Vines says, "The view that the foliage-leaf is the primitive leaf-member, and that the floral leaves are its derivatives, is based upon the fact that, as a rule, the vegetative precede the reproductive organs in ontogenesis. The opposite view, that the most highly specialized floral leaf, the sporophyll, is primitive, is based upon the fact that, phylogenetically, the reproductive precede the vegetative leaves."

Foundations of exact Morphology.

It is refreshing, as Sachs says, to pass from the period of the "Naturphilosophie" to "a chapter in morphology where there is less dogmatism and less poetry, but a firmer basis of observation and induction". The increasing perfection of the microscope, the formulation of the cell-theory in 1838–39, the beginning of embryological inquiries of a more penetrating sort than hitherto, the emergence of a palæontological study of plants, the glimmering light of more concrete evolutionary ideas (Alex. Braun, Unger, Nägeli), and perhaps some healthful influence from the sister science of zoology, combined to strengthen a new movement, about 1840, in the history of the morphology of plants. Reacting from the vagaries of the speculative school, botanists began to take their science more seriously, and the key-note is struck in the title of Schleiden's text-book (1842–43), *Die Botanik als inductive Wissenschaft.*

Matthias Jacob Schleiden (1804–1881), Schwann's colleague in Jena and one of the founders of the cell-theory, did much anatomical and embryological work, but his chief historical importance is probably expressed in his text-book, with the suggestive title already cited, which came as a tonic to his times. "The difference", Sachs says, "between this and all previous text-books is the difference between day and night." Schleiden was a combative critic, whose own work gave solidity to his polemic, and who certainly did much to re-assert the dignity of botany—*as an inductive science.*

Another leading spirit in the new movement was Carl von Nägeli. He did much to clear up the phenomena of cell-formation, and may almost be said to have introduced the "apical cell" to botanists; he laboured

with true morphological insight at the lower Cryptogams, Algæ in particular; and both as a pre-Darwinian and an anti-Darwinian he is of great interest in the history of evolution theories.

Comparative Embryology.

Although the study of the development of plants had been well begun by Wolff, Brown, and Schleiden, the history of the flowering plant's embryo was still obscure, and the development of flowerless plants or Cryptogams was in great part unknown. In other words, botany was awaiting its Von Baer who should establish comparative embryology. The credit of achieving this rests mainly with Wilhelm Hofmeister.

From 1849 onwards Hofmeister published a brilliant series of researches, in which he worked out the early stages in the development of both flowering and flowerless plants, and, much more than that, unified no small part of the whole by detecting the alternation of generations which dominates a long series of plants from liverworts to Dicotyledons. "The results", Sachs says, "of the investigations published in the *Vergleichende Untersuchungen*, in 1849 and 1851, were magnificent beyond all that has been achieved before or since in the domain of descriptive botany" . . . "the idea of what is meant by the development of a plant was suddenly and completely changed" . . . "alternation of generations, lately shown to exist, though in quite different forms, in the animal kingdom, was proved to be the highest law of development, and to reign according to a simple scheme throughout a long series of extremely different plants" . . . "the reader was presented with a picture of genetic affinity between Cryptogams and Phanerogams, which could not be reconciled with the then reigning belief in the constancy of species" . . . "what Hæckel, after the appearance of Darwin's book, called the phylogenetic method, Hofmeister had long before actually carried out, and with magnificent success."

It need hardly be said that some of the finest morphological work of the Victorian era has been inspired by, and founded on, Hofmeister's remarkable achievements.

Thus, in a recent retrospect Prof. Marshall Ward writes as follows:—

"Bower and Campbell have laid bare, by their indefatigable labours, the histological details of the Mosses and Vascular Cryptogams, and carried the questions of alternations of generations and the evolution of these plants so far, that it would almost seem little remains to be done with Hofmeister's brilliant conception but to ask whither it is leading us; the genetic relationships have become so clear, even to the details, that the recent discovery by Ikeno and Hirase of spermatozoids in the pollen-tubes of Cycas and Gingko, almost loses its power of surprising us, because the facts fit in so well with what was already taught us by these and other workers".

Alternation of Generations.

The idea of alternation of generations came to botany from zoology through the influence of Steenstrup's famous essay. It was established by Hofmeister (1851) in regard to mosses, ferns, conifers, and the like, where he showed the regular alternation of a sexual and a spore-bearing generation. The sexless "fern-plant" produces spores; these develop into minute sexual prothalli, from the fertilized ova of which the "fern-plants" arise. The sexual "moss-plant" produces ova and spermatozoa; from the fertilized ovum there springs a "moss-capsule", which remains attached to the "moss-plant", but is a separate generation producing spores; the spores germinate and form a thread-like protonema, from which the "moss-plant" arises. In our modern terminology, there is an alternation between a sexual gametophyte and an asexual sporophyte. But although the general idea is clear enough now, it has had an intricate history, and there are still many unsolved problems. In fact, as Dr. Scott has said, it remains "the greatest mystery in the morphology of plants". From a scholarly historical sketch by Dr. W. H. Lang I have selected the following notes on the development of the idea:—

At first, the only alternation recognized in plants was the alternation between vegetative shoots and reproductive shoots or flowers, which is a different question. In 1851 came Hofmeister's monumental work. In 1856

Pringsheim extended the recognition of alternating generations to Algæ (*Œdogonium* and *Coleochæte*), and in 1866 Hæckel gave a clear generalized account of the subject in his *Generelle Morphologie*, introducing the convenient term *metagenesis* for true alternation of generations as opposed to such cases as the succession of vegetative and reproductive shoots.

In 1868 Celakowsky introduced a theoretical distinction between two kinds of alternation—homologous and antithetic. Homologous alternation was illustrated among the Algæ, where there may be an alternate occurrence of sexual and asexual forms otherwise similar. Antithetic alternation was illustrated by mosses and ferns, where there are two fundamentally distinct generations, *e.g.* the prothallus and the "fern-plant". With this Braun essentially agreed (1875), and it is interesting, in view of recent zoological discussions by Beard and others, to notice his opinion that antithetic alternation is confined to plants.

Of much importance was the discovery of apogamy (Farlow, 1874), the direct production of the asexual from the sexual without the intervention of ova and spermatozoa, and the converse apospory (Pringsheim, 1876), or the vegetative production of the sexual from the asexual without the intervention of spores.

An extended recognition of alternation of generations among Algæ and Fungi, the further study of apospory and apogamy, the interesting discovery that in many cases the number of nuclear bodies or chromosomes in the dividing nucleus of the sporophyte is twice as great as in the cells of the gametophyte, and a few experimental studies, have influenced the development of the theories of antithetic and homologous alternation, but as yet no decision has been arrived at.

"On the homologous theory, the sporophyte is to be traced back to a generation of originally independent individuals similar to those from which the gametophyte has arisen, the almost invariable alternation and the permanent or temporary dependency of the spore-bearing on the sexual generation being subsequent adaptations. On the antithetic theory, the sporophyte is not

derived from free-living individuals of the ancestral algal form, but has a distinct phylogenetic history as an interpolated stage in the life-history."

Though there remains this difference of opinion as to the nature of the alternation, the unification which has resulted from the recognition of metagenesis has been perhaps the greatest achievement of morphological botany.

Hofmeister's main work was an elucidation of the comparative embryology of the moss-like, fern-like, and flowering plants—the Bryophytes, Pteridophytes, and Spermaphytes. It was for others to follow his example by a study of the Thallophytes—the Algæ, Fungi, and Lichens.

Study of Algæ, Fungi, and Lichens.

In regard to the Algæ, a systematic basis had been supplied by such labours as those of the Agardhs, William Harvey, and Kützing; and important observations on their reproduction had been made by Vaucher, Nägeli, Braun, and others. After Hofmeister's work, however, the study of Algæ rose greatly in morphological dignity in the hands of investigators like Pringsheim, Cohn, Thuret.

But the series of Algæ is so immense that even now, after forty or fifty years of steady work, there seems little certainty as to the affinities of the several groups.

In the sixteenth century Hieronymus Bock still spoke of Fungi "as merely the superfluous moisture of the earth and trees, of rotten wood, and other rotten things". "About the middle of the seventeenth century", Sachs says, "Otto von Münchausen thought that mushrooms were the habitations of Polypes, and Linnæus assented to that view." Similar notions existed till late into our own century; in fact, Fungi were almost the last organisms to be in any degree mastered by the naturalist. It almost follows from this that there is no department of botany which has made greater strides during the Victorian era than the study of Fungi. In a presidential address to the botanical section of the British Association (1897), Prof. Marshall Ward outlined the history in masterly fashion:—

"Little more than thirty years ago", he says, "we knew practically nothing of the life-history of a fungus, nothing of parasitism, of infectious diseases, or even of fermentation, and many botanical ideas now familiar to most educated persons were as yet unborn. Our knowledge of the physiology of nutrition was in its infancy, even the significance of starches and sugars in the green plant being as yet not understood; root-hairs and their importance were hardly spoken of; words like *heterœcism*, *symbiosis*, *mycorhiza*, &c., did not exist, or the complex ideas they now connote were not evolved. When we reflect on these facts, and remember that bacteria were as yet merely curious 'animalculæ', that rusts and smuts were generally supposed to be emanations of diseased states, and that 'spontaneous generation' was a hydra not yet destroyed, we obtain some notion of the condition of this subject about 1860."

As Marshall Ward points out there were early workers of great merit, such as Fries—the Linnæus of the Fungi; the Tulasnes, who began the elucidation of intricate life-histories, such as that of ergot; and Berkeley, who "linked the period previous to 1860 with the present epoch"—but it was to the genius of De Bary that we owe the first great steps towards an *understanding* of the Fungi:—

"If I may compare a branch of science to an arm of the sea, we may look upon De Bary's influence as that of a Triton rising to a surface but little disturbed by currents and eddies. The sudden upheaval of his genius set that sea rolling in huge waves, the play of which is not yet exhausted. . . . His development of the meaning of sexuality in Fungi, his startling discovery of heterœcism, his clear exposition of symbiosis, and even his cautious and almost wondering whisper of chemotaxis were all fruitful."

With De Bary's name is also associated one of the most remarkable botanical discoveries of the second half of the nineteenth century, namely, that "Lichens are not a class co-ordinating with the Algæ and Fungi, but a division of Ascomycete Fungi which have this peculiarity, that they spin their threads round the plants on which they feed and take them up into their tissue." In other words, lichens are dual plants, illustrating symbiosis between fungoid and algoid partners. De Bary's sug-

gestion was adopted and elaborated by Schwendener, and its correctness was further demonstrated by Bornet, Stahl, and others. In spite of the opposition of many eminent lichenologists, the "dual hypothesis" has now general recognition.

Chapter VI.

Physiology of Animals.

The Problem of Physiology—Ancient Physiology—Aristotle—Galen—Mediæval Physiology—Harvey—Physiology comes of Age as a Specialism: Haller—Physiology becomes Comparative—Advance of Comparative Physiology—Chemical Aspects—Physical Aspects—Du Bois-Reymond—Experimental Physiology—The Study of Internal Secretions—Analysis of Nervous Mechanism—Cellular Physiology—The Protoplasmic Movement—Pathology—Reproduction in Animals.

The Problem of Physiology.

The physiologist is pre-eminently an investigator of vital *activity*. Whether he studies the leaf of a plant or the lung of an animal, a single cell or an entire organism, his question always is, "*How does this live and work?*" He studies structure too, but only as a means to an end, that he may understand function better. In one of his lectures, Prof. Burdon Sanderson illustrated the physiologist's attitude by the characteristic question, which came to Clerk Maxwell's lips when, as a boy, he was shown some mechanism, "What is the *go* of this?", or, if put off by some verbalism, "But what is the *particular go* of it?"

Starting with *the organism as a whole*—an intact creature with habits and temperaments, the physiologists have proceeded, slowly but persistently, to investigate the functions of its *organs*, the properties of its *tissues*, and the phases observable in its *cells*, finally reaching to the full length of the biological tether in the distinctively modern study of *protoplasm*. It need hardly be said that there is still physiological work being done

at all the levels of analysis, and that at none is there anything approaching completeness.

Ancient Physiology.

One of the roots of physiology is in the lore of the old physicians. This was at first, doubtless, either empirical or superstitious, but it began very early to take more rational form. Thus Hippocrates (460–377 B.C.), who was a "priest-physician" at one of the famous Æsculapian hospitals or temples of health, usually gets the credit for trying to place the study of medicine on a scientific, as opposed to a superstitious basis. The other root of physiology is to be found in speculative attempts to formulate some theory of organic life. These attempts oscillated between extremes of materialistic and spiritualistic hypotheses, but it seems hardly possible to speak of an observational basis before the time of Aristotle.

Aristotle.

The interest of the Aristotelian physiology is twofold; it represents an attempt to understand the activities of the body in their relations to one another, and it was to some extent based on observation. To one who had seen the *punctum saliens* (the beating heart) in the embryo-chick within the egg-shell, who knew of the parthenogenesis of bees and the quaint discharge of an arm in cuttle-fishes, who discerned that the fœtus got its food-supplies from the maternal blood through the umbilical cord, the functions of the body were not likely to be treated of in the easy-going fashion which characterized his predecessors. Yet his mixture of truth and error is extraordinary. Aristotle connected all the functions with the animal heat, which he believed to be associated with the blood and centralized in the beating heart. The blood is recuperated by the food in the gut, is kept fluid by the heart's heat, is carried in the pulsating vessels, and not only nourishes the organs, but gives them mobility and sensitiveness; the urine is derived from the blood flowing in the kidneys; the brain is bloodless and produces mucus; the sense-organs are in the head so that they may not be overheated by the blood; the heart is the seat of the soul and its controlling agencies.

It is generally allowed that Galen (132–200 (?) A.D.)

was the first to realize the dignity of the physiologist's calling, maintaining that the art of medicine must rest on a science of physiology, and that physiology without a secure anatomical groundwork was as a house built upon the sand. It was with these convictions that he so assiduously dissected and experimented on monkeys and swine, the human body being then a forbidden subject. He showed, simply enough, that the arteries contain, not air, but blood; and he recognized what remained obscure to Aristotle —the meaning of the brain and nervous system. "He was also the first to point out that the nerves of sensation are distinct from those of motion, and are connected with different parts of the nervous system" (Rutherford). He followed Aristotle in striving after a connected system of physiological interpretation, and explained the functions of the body as due to the co-operation of the animal spirit (πνεῦμα ψυχικὸν) in the brain and nerves, the vital spirit (πνεῦμα ζωτικὸν) in the heart and absorbed from the air by the lungs, and the natural spirit (πνεῦμα φυσικὸν) in the liver, &c. He elaborated a pathological doctrine of nine temperaments, which has hardly been improved upon since. His system has only historical interest now, but we must remember that it dominated both theory and practice until the sixteenth century.

Galen.

With the revival of learning came a re-awakening of physiological interest, but for many years no real advance was made. A minimum of observation was combined with a plethora of speculation. Most characteristic, perhaps, was the tendency to invent explanations of function in terms of animal and vital spirits.

Mediæval Physiology.

Rising by force of genius high above his contemporaries was Philippus Aureolus Theophrastus Paracelsus Bombast, of Hohenheim (1493 (?)–1541), charlatan and thinker. He seems to have been a fascinating personality—a traveller, who, as he said, "turned over the leaves of Europe, Asia, and Africa, and in so doing suffered much hardship"; a scholar, who learned alike from sage and gipsy, classic and wizard; a democrat, who said, "Get thee behind me, Greek, Latin, and

Arabic", and by lecturing in German "sent a new thrill through the untaught bosoms of the people". It was probably from the East that Paracelsus derived his doctrine of the Archæus, the determining force of life, the "spiritus rector" of the body, the "vital force" of later days. It was an early expression of the fact which still confronts us, that the organism has a secret!

Paracelsus did not achieve much, but to him, and to his follower Van Helmont (1577–1644), who invented the word *gas*, and suggested the theory of digestion by ferments, was largely due the overthrow of the Aristotelian and Galenian traditions which had outlived their usefulness.

Thus Paracelsus gave a death-blow to the old pathological doctrine of the four "humours". The revival of the study of anatomy by men like Andreas Vesalius (of Wesel), and Fabricius, whose names are perpetuated in connection with various organs of man and animals, was another factor in progress. Throughout the long history, anatomy has again and again proved the sheet-anchor which has kept physiology in safety.

Harvey.

The doctrines of Aristotle and Galen—valuable for their age—had gradually become an inhibiting dogma, and the strength of tradition often broke the young spirit of discovery. It is to Harvey (1578–1657) that we must give the credit of inaugurating a new epoch of observation and experiment. It was not merely that he demonstrated the circulation of the blood, and analysed out some of the dynamic factors in the flow; it was his careful method of observing and experimenting, instead of guessing and theorizing, that gave him his high historical import. He comes into line with Copernicus and Galileo, Bacon and Descartes, and the other founders of the scientific method.

Physiology comes of age as a Specialism.

The return to observation and experiment, which we associate with the name of Harvey, was rapidly rewarded by many discoveries. Some idea of the dignity of the subject began to dawn in the minds of workers, and it soon became necessary to gather what was securely known into a system—better than that of Galen. This was achieved

by Albrecht von Haller (1708–1777) in his *Elementa Physiologiæ Corporis Humani*. Educated under Boerhave of Leyden, he became professor at Göttingen in 1736, and for seventeen years taught anatomy, botany, medicine, and surgery.

Prof. W. Rutherford characterizes Haller's position in a sentence: "Possessed of a strictly logical mind, strongly inclined towards physics and mathematics, he insisted on eliminating from physiology all statements that could not be verified by observation and experiment; he added considerably to the store of physiological facts, arranged them in the logical order of science, and thus gave to physiology its present aspect".

We may regard the publication of Haller's great work as marking the date when physiology came of age as a specialism. Haller is also of historical interest for his early researches on respiratory movements, the contractility of muscle, the irritability of nerves, and many other problems, and for the authority which he lent to two doctrines—the Preformation-theory of Development, and the theory of a Special Vital Force, which, in their cruder forms at least, were erroneous and disastrous.

Among the many noteworthy advances which mark Haller's period, we may select two. The study of irritability, which Francis Glisson (1597–1677) had begun almost a hundred years before, was continued by Haller, by John Brown (1735–1788), by Galvani (1737–1798), who discovered animal electricity, and so one gradually passes to Sir Charles Bell (1774–1842), who distinguished the sensory and motor (or afferent and efferent) functions of the dorsal and ventral roots of the spinal nerves, and to Marshall Hall's elucidation of nervous reflex action, which brings us close to the work of to-day.

On another line, however, there were no less momentous steps of progress. The discovery of oxygen by Priestley (1733–1804) and Lavoisier (1743–1794) led Girtannier (1760–1800), Black, and Mayow to sound views on the chemical nature of respiration, and thus one of the πνεύματα (spirits) of the old physiologists became at length objective and measurable.

The earlier physiologists concerned themselves almost wholly with the functions of man and mammals; and even now the physiology of the lower animals lags far behind, and that of plants still further. It was in the hands of Johannes Müller (1801–1858) that comparative physiology fairly began. A genius beyond doubt, and with the widest of interests, he was especially distinguished by the ease with which he turned from one method to another in seeking to solve a problem. Now he would appeal to physics and again to psychology, here he sought the chemist's aid and there the embryologist's; he tried all methods to gain his end. In showing how animals of high and low degree shed light upon one another, he founded comparative physiology, and gave a new dignity to zoology.

Physiology becomes Comparative.

One is somewhat ashamed to speak of the advance of comparative physiology, for so little has been securely achieved. It is only in contrast to the ignorance of the subject in pre-Darwinian days that what has been done in the Victorian era appears great.

Advance of Comparative Physiology.

There are various reasons why comparative physiology lags so far behind comparative anatomy. There are the intrinsic difficulties of the subject, for the lower we descend in the animal kingdom the more baffling is the study of function, morphological simplicity implying physiological complexity. As Prof. Foster has said: "Physiology is, in its broad meaning, the unravelling of the potentialities of things in the condition which we call living. In the higher animals the evolution by differentiation has brought these potentialities, so to speak, near the surface, or even laid them bare as actual properties capable of being grasped. In the lower animals they still lie deep buried in primeval sameness; and we may grope among them in vain unless we have a clue furnished by the study of the higher animal." The history of the science shows a passage from man to animal, from higher animal to lower animal, and, most tardily of all, from animal to plant.

Another difficulty is consequent on specialization. The

zoologist rarely knows enough chemistry, the chemist rarely knows enough zoology, to enable either to contribute much to comparative physiology. And as for the chemical physiologist, expert as to man and mammals, he has too many pressing problems of his own—with attractive practical outcome too—to be readily tempted aside by the digestive cæca of the star-fish or the mid-gut gland of the snail. One zealous worker in the latter part of the Victorian era deserves to be commemorated, C. F. W. Krukenberg. He realized the dignity of the problem to which he set himself, and the results recorded in his *Studien* and *Vorträge* remain a monument to the industry of an unfortunately short life. Particularly notable too has been the work of Verworn on the Protozoa, which form the *Ultima Thule* of the physiologist. Ingenuity of experiment and fertility in suggestion are characteristic of his work, the results of which are summed up in his stimulating *Allgemeine Physiologie* (2nd ed., 1897).

Chemical Aspects.

Since the time of Johannes Müller the science of physiology has become highly specialized, and it is necessary to distinguish several separate lines of advance which have the common aim of storming the citadel of life.

Thus there is the study of the chemical aspect of vital phenomena, generally referred to, not very happily, as chemical physiology or physiological chemistry. With the beginning of this we may associate the names of Wöhler and Liebig, and the progress of the study should be connected, on the one hand, with the development of organic chemistry, on the other hand, with the deepening of analysis, which forced the physiologist from the investigation of the functions of organs to an inquiry into the metabolism or *Stoffwechsel* of the living body.

To appreciate the importance of even the early steps we must remember that before Liebig's day the majority of chemists held that their laws did not apply in the world of life, and even the great Liebig himself regarded the chemical processes which occur in organisms as distinctly subsidiary to the operations of the *Lebenskraft* or vital force.

It was in 1828 that Wöhler (1800–1882) succeeded in building up the characteristic organic waste product urea from inorganic substances. This step in "chemical synthesis" not only gave an impetus to the study of other organic substances of physiological importance, but it was fatal to at least one form of the prevalent "vital-force theory", according to which organic substances were supposed to be only producible by living organisms. The term "organic chemistry" began to be replaced by "the chemistry of the carbon compounds", which, if longer, has no theoretical implication. Wöhler's synthesis has been followed by many others equally remarkable, *e.g.* of sugar; and various announcements, such as Lilienfeld's, still requiring corroboration, lead us to expect that the synthesis of proteids is not far off.

Another pioneer was Justus von Liebig (1803–1873), the first to attempt a systematic survey of the chemical processes in living organisms. His great work, *Chemistry in its Applications to Agriculture and Physiology* (1840; 8th ed., 1865), is still a classic, and has had an influence only second to that which the author himself had upon a large body of students.

To appreciate the change which has taken place since Liebig began his work, one has only to take an old physiological text-book, with its minimum of chemistry, and compare it with a good modern book such as Bunge's or Halliburton's.

For many years what was done was in the main *physiological chemistry*—analysing, naming, and recording the distribution of organic substances in the body, all very well in its way, but not very definitely physiological. More recently, however, what has been done has been more clearly *chemical physiology*, that is to say, an association of the chemical composition of the substances studied, with the vital phenomena in which they are, to say the least, implicated.

For another line of physiological progress it is more difficult to find a name. By analogy it should be called

Physical Aspects.

physical physiology, or physiological physics, but both seem absurd. We mean the study of the physical aspects of vital phenomena, the trans-

formations of energy in the body, the problems of animal heat and body-temperature, the dynamics of the circulation, animal electricity, the mechanics of movement, the optics of the eye, the acoustics of the ear, and so on; in short, the study of all those phenomena associated with life which admit of being studied and measured by the methods and instruments of experimental physics. Perhaps it may be said that the whole body of research in this direction is centred in the doctrine of the conservation of energy which Joule and Mayer established, and which was shown by Helmholtz and others to hold true for the living organism as well as for the dead engine.

Du Bois-Reymond.

Among those who have welded the contact between physics and physiology, and equally, perhaps, among those who have vindicated the biological standpoint in modern culture, Emil du Bois-Reymond (1818–1896) ranks high.

He was interesting personally as a man of versatile genius, as a loyal German patriot of French descent, and as one of the many who have reacted from Theology to Science, doubtless to the benefit of both. After a period of interest in geology he found himself, along with Helmholtz and many other afterwards illustrious workers, at the feet of Johannes Müller, whose chair he eventually filled.

Taking up the clues which Galvani and Volta had first handled about the end of the eighteenth century, and which many had tried to use, Du Bois-Reymond devoted his life to the study of the electromotor phenomena associated with muscle and nerve. There are electric currents in these tissues, and alterations in the currents during functional activity. By working out the intricate details of this thesis, now so familiar to students of medicine; by the more general application of physical methods to physiological problems; by introducing ingenious instruments; and by establishing (after many years of sorry quarters) a truly wonderful Physiological Institute, he did great service to physiology.

In spite of his lifelong devotion to one main problem,

Du Bois-Reymond was keenly interested in history and philosophy, literature and art. Like Huxley, from whom he differed in most ways very markedly, he excelled as a lecturer, impressive even to those who disagreed, for his French elegance of style, his Celtic dramatic power, and his strongly developed historical sense were for the time irresistible. An evolutionist and a materialist of a refined sort, he did good service in ridding physiology of the cruder forms of Vitalism, though how far he touched the position of the subtler "Neo-vitalists" is a matter of opinion. In any case he showed the fallacy of the strongly engrained impression that science presumes to give more than proximate explanations of facts.

Experimental Physiology.

Although physiology may become experimental at almost every turn, the phrase "experimental physiology" may be used in a more restricted sense in reference to experiments on living creatures. Whether we put caterpillars into a gilded box and watch for a change in the colour of the pupæ, or feed tadpoles with different kinds of food to show that nutritive changes affect sex, or extirpate the thyroid gland of a rabbit to see the effect on the constitution, or stimulate the nerve-centres on the brain of a chloroformed monkey, we are making experiments on living creatures. [It is here that the problem of the ethical limits of scientific inquiry is raised in many minds, but it should not be restricted to this issue.]

Though the experimental method was long ago resorted to by Harvey, it practically dates from the work of Magendie (1783–1855) and Claude Bernard (1813–1878). In illustration of its use we may refer to the work on internal secretions and on the nervous mechanism, both very characteristic of modern physiology.

The Study of Internal Secretions.

This unattractive title expresses one of the most significant of recent advances in modern physiology. The study has to do with the action of various glands on the blood that passes through them, and its beginning dates from Claude Bernard's discovery of "the glycogenic function of the liver". While older physiologists had been more or

less content to interpret the liver as an organ for secreting bile (now regarded as for the most part a waste-product), Bernard detected a much more important activity, namely, that the liver utilizes the sugar brought by the blood from the food-canal to build up a reserve product, glycogen or animal starch.

Thereafter came many interesting advances, gropings, and stumblings, but in 1889 a step was taken by Minkowski so firm and definite that it gave stability to a whole series of similar investigations. This step concerned the pancreas, which is well known to be a most important digestive gland, secreting a juice which attacks all the three kinds of food—carbohydrates, fats, and proteids. Minkowski demonstrated that phenomena of diabetes followed extirpation of the pancreas; and as one of the features of this disease is the appearance of sugar in the urine there was here an opportunity for precisely proving and exactly measuring at least one of the results of tampering with the organ in question. In short, Minkowski proved that the pancreas, besides being a digestive gland, exerts an essential influence on the blood which passes through it.

Minkowski's discovery gave an impetus to the study of other organs, notably the thyroid gland. Various theories had been hazarded in regard to its function, but probably the most general opinion was that it was not of any great importance. Gradually, however, observations accumulated showing that degeneration of this organ was associated with goitre, Derbyshire neck, and cretinism; that its absence was the structural fact implied by the disease of myxœdema; and that all these diseased states could be ameliorated or temporarily cured if the patient compensated for the degeneracy of his own organ by eating that of sheep, &c., or receiving injections of the thyroid extract of his companion mammals.

We had smiled at the ancients for recommending the coward to eat the lion's heart, and for many similar prescriptions; yet here were the cautious nineteenth-century physicians injecting thyroid extract in order to cure myxœdema, or to stimulate the retarded de-

velopment of the cretin, and with most successful results.

We cannot follow the history; it is enough to say that although much remains uncertain as to what exactly the thyroid, with its internal secretion, does to the blood, there is no doubt that this inconspicuous organ does something essential in keeping the blood and nervous system up to a certain standard of efficiency.

Another characteristically modern physiological movement has been the analysis of the nervous mechanism which determines alike the behaviour of animals and the conduct of man. This is the supreme and the most baffling problem of the physiologist, and he has moved towards its solution along two paths which have led him to results sometimes congruent, and yet often discrepant, encouraging and yet warning him at every turn.

Analysis of Nervous Mechanism.

One of the two paths is experimental, and among those who have moved most steadily along it are Ferrier, Fritsch, Hitzig, Munk, Goltz, and Horsley. One of their main aims and, to some extent, achievements, has been the localization of certain functions in certain parts of the brain, and along certain tracts of the nervous system. The inquiry was begun by Willis, but in the period between him and Horsley even the language has changed.

The other path is histological—the attempt by microscopic analysis to find a way through the extraordinary maze of cells and fibres which form the brain and spinal cord. Albert von Kölliker was one of the most illustrious pioneers, and even as veteran he has not ceased to lead. No small part of the progress, however, has been due to the discovery of new methods which we especially associate with the names of the Italians Golgi and Marchi, and the Spaniard Ramon y Cajal.

Cellular Physiology.

The cell-doctrine of Schwann and Schleiden (1838–9) was not merely a morphological generalization (that all organisms have a cellular structure), it was also a physiological theory which sought to express the function of an organ in terms of the changes

in the component cells. Perhaps one might say that the suggestion was, that the cell was in organic processes like the molecule in the inorganic world.

The investigation of the structure of cells soon outran the physiological interpretation of that structure; for it must be universally confessed that a group of cells—in a ganglion, or a digestive gland, or a kidney—performs functions which we are often quite unable to connect in any luminous way with the known facts about their organization or mutual relations. On the one hand, we see complexities of cell-structure whose meaning is unknown or uncertain; on the other hand, we observe functions which we cannot correlate with any known organization.

This double break-down has led many to adhere to Huxley's statement (1853), "The cells are no more the producers of the vital phenomena than the shells scattered along the sea-beach are the instruments by which the gravitative force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted."

On the other hand, if we avoid word-quibbles, and define the cell as a unit area of living matter (cytoplasm and nucleoplasm); if we study the phenomena of cell-life in that natural analysis which is afforded us by the unicellular organisms; if we carefully estimate what is known as to complex internal organization of cells and its changes with change of function and external conditions; we may perhaps advance to a more hopeful position—that cellular physiology is rather beginning than ended.

Although we do not know the whole meaning of the nucleus, we know from the experiments of Balbiani, Gruber, Bruno Hofer, Verworn, and others, that a maintenance of the inter-relations between nucleoplasm and cytoplasm is essential to the continuance of cell-life. We cannot explain the activity of the nerve-cells, but the discovery of their dendritic ramifications and extraordinary complication of inter-relations has *some* meaning to us. Or, again, that an exhausted nerve-cell should show more or less nuclear collapse (Hodge,

Mann, &c.) is surely a beginning of knowledge which promises much.

The Protoplasmic Movement.

It must be confessed, however, that the physiological part of the cell-theory has not as yet justified itself to the extent that its founders evidently expected. In any case, the ultimate problem of physiology is *within* the cell, in the metabolism of the complex substances which compose it. Thus we reach what Prof. Foster has called "the protoplasmic movement", the concentration of research on the chemical changes of the complex substances which appear to form the physical basis of life. We shall return to this in the chapter on "Cell and Protoplasm".

Pathology.

Since pathology, or the science of deranged function, is strictly a department of physiology (which has to do with *all* vital functions), its history is naturally somewhat similar.

(1) In ancient days, diseases found theological or metaphysical interpretation, in terms of evil spirits, morbid entities, conflicting temperaments, and the like. There was, in other words, an attempt at a pathology of the entire organism, which must come last, not first.

(2) Some early workers, such as Aretæus of Cappadocia, in the time of Vespasian, or Galen in the second century, got their feet firmly planted on the solid ground of anatomy, and made great strides on the scientific path. But the overthrow of the Roman Empire and other great changes arrested progress in this, as in other departments of biological research, for about fifteen centuries.

In the scientific renascence pathology shared. Diseases were traced to various regions of the body, *e.g.* head, chest, and abdomen. Morgagni (1682–1771) at Padua began the precise localizing of disease in organs. John Hunter founded what was practically the first pathological museum; and Andral (1797–1876) raised morbid anatomy to the level of an "interpreting science".

(3) So far, pathology had been based for the most part on the naked-eye morbid anatomy of organs, but the progress of anatomy and physiology soon made a

deeper foundation possible. "The dawn of the new era", Prof. Greenfield says, "may be traced to the beginning of the present century, and may be said to have begun with new ideas of structural anatomy preceding the fuller knowledge of function. For, until the primary analysis of the structure of the body had been made, until the minuter elements had been grouped into classes, and their individual functions and powers determined, it was impossible to reduce to any general expression the derangements to which they were subject. The first step to this was the re-arrangement and classification of the tissues, due partly to Haller, but mainly to the genius of Bichat, who must be regarded as the founder of general morbid anatomy, as well as of general anatomy. He not only classified the tissues and organic systems, but he entered into their pathology, and asserted that 'each tissue has its own diseases'." Mere localization of disease in organs was demonstrably insufficient after Bichat had shown that different tissues in the same organ might be the seat of different pathological changes.

(4) But analysis could not long rest at the level of tissues, and the formulation of the cell-theory marks a new era in the history of pathology. Johannes Müller, who moved on so many different lines of research, attacked the problem of the histology of tumours; and Goodsir was, in Virchow's words, "one of the earliest and most acute observers of cell-life, both physiological and pathological".

To F. G. J. Henle (1810–1885) belongs the credit of having founded the Modern Pathology which Virchow took the lead in developing. A pupil of Johannes Müller, and contemporary with Schwann, he published in 1846 a *Manual of Rational Pathology*, in which he systematized, *in their physiological relations*, the facts then known, maintaining for the first time clearly that "physiology and pathology are branches of the same science". He should also be remembered for his remarkable prevision (1840), that contagious diseases must be due to "parasitical beings which are among the lowliest, smallest, but at the same time most productive which

are known". This was partly based on Schwann's researches on fermentation and putrefaction, and on Bassett Audouin's proof that the muscardin disease of silkworms was due to a *contagium vivum.*

The classic monument of this fourth level of analysis is, however, Virchow's *Cellular Pathology* (1858), in which he showed that disease may often be localized in cell-systems and cell-territories, and sought to express both morbid growths and morbid stages in terms of abnormal cell-multiplication and reaction. "Nothing", Prof. Greenfield says, "could have been further from the central idea of Virchow's teaching than the mere mechanical application of cellular structure to the elucidation of the phenomena of life and of disease. It is the living cell, endowed with vitality and with function, governed by laws of existence, capable of self-multiplication and propagation, and arranged in organic systems, which he studies. It is the cell as the living active agent in the production of disease, and the arrest or perversion of its action by disease-producing causes, which have the highest place in his thoughts." The author of the famous dictum, *omnis cellula a cellula,* has said of his own work, "I blocked for ever the last loophole of the opponents, the doctrine of specific pathological cells, by showing that even diseased life produced no cells for which types and ancestors were not forthcoming in normal life".

As with physiology, so here, there is still work being done, and much to be done, at the four different levels of interpretation which represent historical stages. We have still to do with the pathology of the entire *organism*—with the problem of attaching definite meaning to such phrases as "constitution", "congenital tendency", "diathesis", and the like. And it is not easy to avoid verbalism on the one hand, and a violation of the unity of the organism on the other. We have still to do with the pathology of *organs,* which has hardly passed beyond man and the more important domestic animals. Roux's suggestive conception of "the struggle of parts within the organism" remains but little worked, and the relations of disease-variations to those which form

or have formed the raw material of evolution remain obscure. The literature of the pathology of *tissues* and *cells* grows annually like an unending encyclopædia.

(5) The final step in pathological analysis leads, as in physiology, to the study of the metabolism of protoplasm. For it is here that deranged function and normal function have their foundation. As yet, however, the step has been, as it were, into the darkness, with faint glimmerings of light which suggest the possibility of a new pathology and a new therapeutics.

As a fine example of comparative pathological work which is at the same time distinctively biological, we may refer to Metschnikoff's epoch-making researches on phagocytosis.

Reproduction in Animals.

There is as yet only a rudimentary physiology of reproduction either as regards plants or animals. What is called the physiology of reproduction is usually a descriptive account of the processes by which eggs and male elements are formed, liberated, and brought together, and to this there is usually appended some theory of the nature of fertilization and the determination of sex. But the descriptive account is only a needful preliminary, it does not deal with the relation of reproduction to the general metabolism of the body; and we are as far from understanding the physiological meaning of fertilization, or the conditions which lead one fertilized ovum to become a male, and its neighbour to become a female organism. Of theories there has been a profusion, and some of them may have a suggestive value, but the majority of the earlier ones are mystical and absurd, and the majority of the later ones hopelessly partial. *The Evolution of Sex* (1889) contains a preliminary attempt to unify the various sets of phenomena by restating them in terms of protoplasmic metabolism.

Perhaps no scientific problem has been viewed with more interest by outsiders than that of the determination of sex, that is, the analysis of the conditions which determine whether an ovum shall develop into a male or a female offspring. The interest is, of course, due

to the practical importance of the question in connection with man and domesticated animals. The number of speculations on this matter and on the general nature of sex has been well-nigh doubled since Drelincourt, in the last century, brought together two hundred and sixty-two "groundless hypotheses", and since Blumenbach quaintly remarked that nothing was more certain than that Drelincourt's own theory formed the two hundred and sixty-third. Subsequent investigators have, of course, long ago added Blumenbach's to the list, which is still mounting up.

It must not be supposed that all the many theories as to the determination of sex have been merely armchair musings, for numerous experiments and observations have been made by breeders and physicians. What vitiates almost all, however, is the fatal defect, that, while attending to one factor, *e.g.* the relative age of the parents, the relative vigour of the parents, the nutrition of the embryo, no sufficient care has been taken, and in most cases no attempt has been made, to eliminate other probably operative factors, either experimentally or by statistical devices. There is at least a strong probability, that every ovum of an organism with separate sexes has from the first a predisposition towards becoming a male or towards becoming a female, but that this predisposition may be altered by the nutrition of the ovum, by changes in the period before fertilization, by fertilization itself, and by environmental influences (of nutrition, temperature, &c.) during embryonic or even larval life, until the period is reached when the sex of the offspring is fixed. We cannot, and need not, discuss the problem here (see revised edition of *The Evolution of Sex*, 1899); we wish simply to point out the probability that many factors determine the result, and that insistence upon one alone (*e.g.* Prof. Schenk's insistence upon the diet of the mother) is almost certain to be fallacious.

Chapter VII.

Physiology of Plants.

Empirical Stage—Influence from Animal Physiology—Nutrition in Plants—Movement and Feeling in Plants—Sachs—Reproduction in Plants—Ancient Conjectures as to Sexuality of Plants—Camerarius—Kœlreuter—Sprengel—The Act of Fertilization—Sexuality of Cryptogams—Experiments on Sex and Reproduction.

Empirical Stage.

The lore of the gardener embodied from ancient times not a little knowledge which we would now call *physiological*, but it was long in acquiring scientific value. It is impossible to believe that the old practice of caprification (concerned with the pollination of the fig), or the equally ancient device of dusting the female date-flowers with pollen, were in any real sense understood; and the same must be said of simpler matters, such as pruning and manuring. The old lore was empirical and not scientifically understood.

Influence from Animal Physiology.

Just as discoveries as to the functions of the human body raised inquiry in regard to the functions of animals, so the facts of animal physiology have from time to time prompted the botanists to look for similar phenomena in plants. Thus Harvey's discovery of the circulation of the blood raised the question as to the movements of the sap. On the whole, it must be confessed that vegetable physiology has always lagged behind animal physiology, and this is not unnatural, since there is much less division of labour in the plant than in most animals, and the analogy of the human body, always suggestive to the animal physiologist, is hardly relevant.

Nutrition in Plants.

There are few more striking examples of the slow and often devious progress of science than the history of the physiology of nutrition in plants. The details are skilfully set forth in Sachs's *History of Botany*, on which the following summary is based.

The Aristotelian theory that the food of the plant is prepared for it in the ground seems now crude enough,

and yet the "humus-theory", which persisted into the nineteenth century, was as grossly erroneous. It may be noted, however, that what we now know in regard to the rôle of bacteria (not to speak of earth-worms) in preparing the soil-food for plants might be used to rehabilitate both the Aristotelian conjecture and the humus-theory.

Towards the end of the sixteenth century (1583) Cesalpino broke away from the bondage of Aristotelian tradition. He compared the vessels and fibres of plants to the veins in animals, and suggested that the food passed into and through the plant by a sort of suction, as oil in the wick of a lamp. Joachim Jung also marks the growing revolt. He insisted that the plant took an active part in its own nourishment, and suggested that the nature of the openings in the root might be such as to admit only what was of advantage. The chemist Van Helmont (1577–1644) deserves to be remembered in this connection as the author of the first recorded experiment in vegetable physiology. He planted a willow in a weighed quantity of soil and watered it with rain; in five years the plant had grown from 5 lbs. in weight to 164, while the earth in the pot showed only a loss of 2 ounces. Not suspecting that the plant drew a great part of its food from the air, he was forced to exaggerate the virtues of rain-water.

J. D. Major (1639–1693) is generally referred to as the founder of the theory of circulation in plants—a subject of discussion all through the eighteenth century, and by no means beyond dispute still; but we reach firmer ground in the work of the keen-sighted histologist Malpighi. To him is due the first suggestion of the fundamental fact that the leaves elaborate the crude sap; he believed that this passed from the roots to the leaves by the fibrous elements of the wood; and his only gross error was in regarding the wood-vessels as respiratory air-tubes.

Equally important were the conclusions of the physicist Mariotte (d. 1684), who maintained, for instance, that different plants draw the same material from the soil, but make different stuffs out of it; that the entrance

of water into roots may be compared with its rising in capillary tubes; that the endosperm in the seed may be likened to the yolk in an egg; and that the prevalent conception of a vegetable soul was a gratuitous hypothesis.

A few experiments by John Ray showing the upward passage of sap in the wood and its lateral movement as well; Woodward's measurements showing how much water a mint may take up by its roots and discharge by evaporation; Christian Wolff's acute observations on the exhaustion of the soil after much has been grown on it, and on the variety of matters contained in rain-water—are all of interest, but they are "thrown into the shade by the brilliant investigations of Stephen Hales (1677–1761), in whom we see once more the genius of discovery and the sound original reasoning powers of the great explorers of nature in Newton's age" (Sachs). His *Vegetable Statics* (1727) may be called the foundation-stone of plant physiology.

Hales deserves a most honourable place in the history of physiological botany, not merely because he was a pioneer at an early date, but because he indicated the only sure path of progress. He brought rigorous physical methods to bear upon a biological problem. By ingenious experiments and careful measurements he "made his plants themselves speak". His investigations on the ascent of sap remain of interest, and he was the first to prove that a great part of the food of plants must be derived from the air. It must be remembered, of course, that physics and chemistry had made some progress, else Hales could not have secured his foothold.

In spite of the admirable beginnings made by Malpighi, Mariotte, and Hales, vegetable physiology degenerated for nearly half a century into profitless theorizing about circulation and the like. A new impulse was needed, and that came from chemistry, which Lavoisier had begun to reorganize. In 1774 Priestley (1733–1804) had discovered oxygen, and five years later he showed that this gas was, in certain conditions, exhaled by plants. In the same year Ingen-Houss (1730–1799) took an even bigger stride, showing that it is only in the light

and only by the green parts that oxygen is given off, that this is quite distinct from another (respiratory) process in which carbonic acid gas is liberated, and that the chief if not the only source of the carbon in plants is in the carbonic acid gas of the atmosphere.

In 1800 Senebier (1742–1809) corroborated Ingen-Houss's discovery of the decomposition of carbon dioxide. Much more important, however, was the work of Théodore de Saussure (1767–1845), son of the famous explorer of the Alps, who introduced the quantitative method of estimating a plant's income and expenditure, and thereby showed that the elements of water are fixed in the plant as well as the carbon of the carbon dioxide, that respiration is essential to growth and is related to the internal heat (measurable in flowers), that plants are unable to use the nitrogen of the atmosphere, and that there is no normal nutrition apart from nitrates and similar salts in the soil.

The chief representatives of vegetable physiology about 1840 were De Candolle (better known as a systematist), Treviranus, and Meyen, but none of them made any new step of importance. Two impeding theories had to be got rid of, the theory of vital force and the theory of humus. The former could only die hard, but the latter was cut short by Liebig. According to the "humus-theory" it was believed that plants feed upon prepared organic matter (or humus) in the soil, and this was regarded as a source of both carbon and nitrogen. Liebig showed, however, that (Fungi apart) plants derive from the soil only water, ammonia, and inorganic salts, and corroborated the already established conclusion that all the carbon supplies are in the CO_2 of the air. As plants die down they necessarily enrich the soil with humus, but this humus as such forms no part of the food-supply. There is no doubt that 1840, when Liebig published the first edition of his *Organic Chemistry in application to Agriculture and Physiology*, is one of the red-letter dates in the history of biology. It marks the first concrete realization of the "circulation of matter".

What Liebig had shown in a general way was con-

firmed with much greater exactness by Boussingault, whose careful culture-experiments showed that plants do not use the free nitrogen of the air, that they will flourish in soil artificially deprived of organic matter if nitrates are added, that all the carbon in the plant is derived from carbon dioxide, and that various alkaline salts (sulphates, phosphates, &c.) are indispensable to vigorous growth. These were the chief results established, after much vacillation, at the date 1860.

Movement and Feeling in Plants.

Even the most easy-going observers could not fail to notice that many flowers open and close with the growing and waning light of day, that many leaves have a position at night which is different from that which they have at noon, that many plants climb by their stems, like the hop, or by their leaf-stalks, like the clematis, or by their tendrils, like the pea and the vine. Of such movements, as well as of others less obvious, there are records in ancient works.

Yet the history of the subject can hardly be called instructive until within the Victorian Era. There were hundreds of isolated observations, but few experiments; there was almost no success in distinguishing the different kinds of movements (*e.g.* growth-movements and periodic movements); and almost no one succeeded in taking a comprehensive or unified view of the subject.

John Ray (1693) puzzled over the case of the sensitive plant which had been imported from America, and directed particular attention to the influence of temperature on the opening and closing of flowers, and even on the bending of stems towards the light; the French Academician Dodart deserves credit for first detecting any problem in the familiar fact that a stem grows away from, and a root towards, the centre of the earth; and Stephen Hales tackled the general question of the conditions of growth.

About 1750 Linnæus constructed his floral clock—an arrangement of flowers opening and closing with regular periodicity—which made a strong impression on the popular imagination, and he seems to have been the first to apply the term "sleep" to the nocturnal changes

of position in flowers and leaves. Soon afterwards the number of known cases of plant-movement was considerably increased.

The degeneracy of vegetable histology towards the end of the eighteenth century, and the dominance of the vital-force theory, combined to hinder further progress in regard to the movements of plants. A return to scientific method, however, was well marked in the experiments of Andrew Knight (1758–1838), an English horticulturist and worthy successor of Hales. He showed that the upward growth of stems and the downward growth of roots were opposite reactions to the same stimulus—"the force of gravitation"; that when germinating plants were grown on a revolving wheel the radicles were directed outwards, in the direction of the "centrifugal force", and the young stems inwards; that the stimulus supplied by moist earth may affect roots more strongly than that of gravity; that the tendrils of the vine and Virginian creeper grow away from the light (negative heliotropism); and so on.

In 1827, while still a young student, Von Mohl published a remarkable essay on tendrils and climbing plants, "the best that appeared on the subject before Darwin wrote upon it in 1865" (Sachs); Dutrochet extended Knight's experiments with the rotating wheel, and attempted to apply his theory of diffusion to the phenomena of movement; and Brücke in 1848 made a classic research on the sensitive plant, distinguishing the periodic movements from the responses to casual stimulus, and attempting an analysis of both in terms of tension and turgidity. These and other investigations were of much interest, yet Sachs ends his historical survey by remarking that "scarcely any point of fundamental importance in phytodynamics was cleared up before 1860".

Sachs.

There is no greater name in the history of modern botany than that of Julius von Sachs (1832–97), and he has probably had a wider influence than any other. Not only have many of the most prominent living botanists sat at his feet, but his books have brought us all into touch with him. He was

great alike as student and teacher, investigator and writer, and he has left an indelible mark on many departments of botany, on vegetable physiology in particular.

His interest in nature was instinctive, for as a boy he made his herbarium and collection of skulls, and it seems to have developed rather in spite of, than in virtue of, his early education. As far as scientific discipline was concerned, he was little influenced by any of his teachers. In face of great difficulties, for he was "a self-made man", he graduated at Prague in 1856. In the following year he established himself as a *privat-docent* in plant physiology, at a time when, as he has himself said, there was practically no such department of botany, and when it was possible for a critic to remark without great exaggeration, "Two lectures are ample for all there is to say upon that subject".

After holding various posts, Sachs was called to the chair of botany at Würzburg, where he remained for the rest of his life, notwithstanding many tempting offers from elsewhere. In spite of severe ill-health and close devotion to his work as a teacher, he succeeded by his original researches in founding the modern physiology of plants, and wrote four great books.

If ever a man made for progress by writing text-books, it was Sachs. His *Experimental Physiology* (1866) is a fundamental classic, which was afterwards brought up to date by his very different (dictated) *Lectures on the Physiology of Plants*; his *Text-book of Botany* (1868) took the place of Schleiden's *Outlines*, and "did for botany what Gegenbaur achieved for zoology, in presenting the morphological facts of the vegetable kingdom for the first time as a whole"; his *History of Botany*, to which we have been greatly indebted in this little book, is perhaps the most charming, and at the same time philosophical, contribution yet made to the historical literature of natural science.

We cannot within our limits do more than hint at what Vegetable Physiology owes to Sachs. Only the nature of his most important work can be indicated, under four heads.

(*a*) *Contributions to a knowledge of the everyday*

functions of plants. Sachs was the first to show that the starch which Von Mohl and others had recognized as almost universal in the chlorophyll grains (or chloroplasts), is the first visible product of elaboration by the chloroplasts under the action of light, and that it passes from its seat of formation to growing and storing tissues. It may be said that no small part of his life-work was concerned with starch and allied substances. In general terms, he devoted himself to the micro-chemical study of the active tissues, a method now familiar, but when Sachs began his work, quite novel. He applied it in particular to the internal phenomena of germination, and to the movements and changes of formed materials within the plant.

(*b*) *Environmental Stimuli.* Sachs made equally great advances by his researches on the reactions of plants to external stimuli. He defined the optimum temperature for germination, studied the heat-rigor and cold-rigor of sensitive organs, showed that heat as well as light is necessary for the formation of chlorophyll, and analysed the various influences of light, and of some rays in particular. By his investigations of the reactions which occur in response to the stimuli of gravity, light, and moisture he placed the study of the irritability of plants on a secure basis.

(*c*) *Methods.* His great manual dexterity and ingenuity of device enabled him to do exact work with very simple instruments, and some of his appliances are now familiar in the botanical laboratory. He made the first growth-measurer (auxanometer); he devised the simple "hanging-sieve", with which he studied reaction to moisture; and he introduced the "klinostat", for studying the reactions of growing parts to gravity. In connection with methods, we may also notice that he gave great attention to the culture of plants in artificial nutrient solutions, a method begun by Duhamel (1758), and of great importance in the determination of the relative physiological value of the different mineral constituents in the plant's food. Sachs also devised the "Lithium-method" of studying the rate of the passage of water and salts up the stem.

(*d*) *Growth and Development.* The questions which interested Sachs most keenly were concerned with the conditions of growth and development ("physiological morphology"), and he approached these in three ways. (1) In his researches on the influence of the environment, *e.g.* light, he studied some of the normal stimuli to which plant protoplasm reacts. Thus, to take a relatively simple case, he showed that the formation of blossoms depends directly or indirectly upon light and particular rays of light, for it is only by the assimilatory activity of the leaves in light that the particular materials required to produce flowers can be produced; and the development of the flowers is suppressed in plants grown in light which has lost its ultra-violet rays by passing through a solution of quinine. His investigation of reactions to gravity, moisture, &c., have also a bearing upon the same problem. (2) He was first to throw a clear light on the relations between growth and cell-arrangement, maintaining firmly that the former determines the latter, and not *vice versâ*. He also formulated two general laws of cell-division. (3) He held a particular theory of specific organ-forming substances, which find their way to their proper areas within the growing plant. This theory will doubtless be developed in a work (which he left in manuscript) entitled "*Principien Vegetabilischer Gestaltung*" (Principles of Vegetable Form). As far as we understand, in his evolutionary views he agreed with Nägeli rather than with Darwin.

Reproduction in Plants.

In the higher animals some of the facts of sex and reproduction are very conspicuous, and could never be hidden from the observer, though they might be, and often were, misunderstood. Man's own zoological position as a mammal gave him a clue. In plants, however, even the elementary facts of sex and reproduction eluded detection for many centuries. Not that they are in any way concealed, in the higher plants (Phanerogams) at least, for there is no more flaunting sexuality than that of the lily; it was simply that, in its superficial expression, the sexual reproduction of plants is very different from that in animals.

The custom of dusting the female date-palm with the pollen from the male flowers, and the more complicated process of caprification in the case of fig-trees, were doubtless quite empirical at first. By and by they seem to have been dimly understood by a few, as may be inferred from Pliny's description of pollen as the material of fertilization, or from the verses of Ovid; but there was little more than confused conjecture until the seventeenth century. A few experiments would have settled the question, but the day of experiment had not yet dawned.

Ancient Conjectures as to Sexuality of Plants.

Rudolph Jacob Camerarius (1665–1721), professor at Tübingen, showed experimentally (1691–1694) that seeds capable of germination cannot be formed without the co-operation of pollen. His first observations were on the mulberry and the dog's mercury (both diœcious, *i.e.* with separate sexes), and he soon extended his experiments to other plants. He called the anthers the male sexual organs, and the ovaries the female sexual organs, and insisted that these terms were not to be taken figuratively. This would be held as rather rough-and-ready terminology nowadays, but at the time Camerarius was justified in his insistence.

Camerarius.

Joseph Gottlieb Kœlreuter (1733–1806), professor of natural history at Carlsruhe, may be said to link Camerarius with such modern workers as Nägeli. Indeed, as Sachs says, "his works seem to belong to our own time; they contain the best knowledge which we possess on the question of sexuality". "He made the first careful study of the different arrangements inside the flower in their connection with the sexual relation, discovered the purpose of the nectar and the co-operation of insects in pollination, and proposed that view of the sexual act which, with some considerable modification, we must still in the main consider to be the true one, namely, that it is a mingling together of two different substances." He is best known by his extensive and fundamental experiments on hybridization in plants,—experiments which should have exerted an even greater influence than they have

Kœlreuter.

done on the theory of fertilization or amphimixis, on the theory of development, and on the theory of species. Worthy of mention along with Kœlreuter were J. and K. F. Gärtner, father and son, who continued experiments on similar lines.

Christian Konrad Sprengel (1750–1816), who loved botany too well to be a successful rector of Spandau, may be said to link Camerarius to Darwin. In his *Newly Discovered Secret of Nature in the Structure and Fertilization of Flowers*, he expounded and illustrated three remarkable conclusions: (1) that many of the characteristics of flowers—nectaries, markings, shapes, &c., are to be interpreted as adaptations in relation to the insect visitors which secure fertilization or pollination; (2) that cross-fertilization is the rule, not the exception, there being not a few reasons why it is unlikely, if not impossible, that carpels are pollinated by pollen from the stamens of the same flower; and (3) that a large number of flowers are dichogamous, *i.e.* with stamens and carpels ripening at different times, one of the ways in which self-fertilization is prevented. Subsequent experiments by Andrew Knight, by William Herbert (1837), and especially by K. F. Gärtner (1844), disclosed the fact which Sprengel had missed, that cross-fertilization has better results than self-fertilization as regards the number and vigour of the seeds,—a conclusion which Darwin was not slow to use in support of his theory, that the adaptations ensuring cross-fertilization were the outcome of a process of natural selection.

Sprengel.

Pollination is the process by which the pollen is transferred by insects, or by the wind, or otherwise, from the stamens to the stigma. There, stimulated by a sugary secretion, the pollen-grain sends out a tube, the pollen-tube, which grows down the style, and enters the micropyle of the ovule within which the ovum or egg-cell lies. The mingling of elements from the pollen-tube with the ovum is the real act of fertilization, and the first steps in making this clear were taken by Amici. In 1823 he first saw the pollen-tube emerge from the pollen-grain, and by persevering observation

The Act of Fertilization.

for more than twenty years he was able to steer clear of the mistakes which misled Brongniart (1826), Robert Brown (1831), and Schleiden (1837), and to prove (1846) that the egg-cell within the embryo-sac of the ovule is stimulated to development by the advent of the end of the pollen-tube. This was at once corroborated by Von Mohl and Hofmeister, and many details have since been added. Strasburger, in particular, has been successful in working out the intricacies of the process, showing that as in animals, so in plants, fertilization is the intimate and orderly union of two sex-nuclei, the nucleus of the ovum, and one of the nuclei which arise from the originally single nucleus of the pollen-grain. It would take us beyond our present scope to show how Guignard and others have made the parallelism even closer by comparing the preparatory or maturation processes which precede fertilization in plants and animals alike.

Sexuality of Cryptogams.

After the sexuality of Phanerogams had been securely established (1846), attention was turned with fresh confidence to the Cryptogams, in regard to which some important observations had already been made. Thus the antheridia and archegonia of mosses had been compared to stamens and ovaries by Schmidel and Hedwig, and the spermatozoids had been discovered and recognized as such by Unger in 1837. Similar observations had been made by Nägeli (1844) and others in regard to the prothallia of ferns. But there was necessarily great obscurity until Hofmeister discovered the alternation of generations (1849), and showed that "the prothallium in the vascular cryptogams is the morphological equivalent of the leaf-bearing moss-plant, while the leafy plant of a fern, of a Lycopodium and a rhizocarp answers to the capsule of the moss". As yet, however, no one had observed the actual union of the male and female sex-elements in Cryptogams, though many botanists had been on the threshold of this discovery. The observation was first made by Pringsheim in the common fresh-water alga *Œdogonium*, and the fact was immediately confirmed by De Bary.

Much has since been done (*a*) in extending the range

of alternation of generations (see chap. v.); (*b*) in studying the great variety of reproductive processes, both sexual and asexual, which occur in the Algæ and Fungi; and (*c*) in investigating the nuclear changes before and after the union of the sex-cells. The most striking new departure has been the introduction of experimental methods.

Experiments on Sex and Reproduction.

From time to time there have been isolated experimental observations on the physiological conditions of sex and reproduction in plants. Thus we have De Bary's case of starved fern prothallia which only produced antheridia, or the familiar case of the yeast plant, which usually multiplies by buds, but produces spores when starved. But no connected series of experiments was ever undertaken until Dr. G. Klebs took the subject in hand. His work, published in 1896, is a fine instance of the success which attends an adherence to scientific method. With great care and patience he experimented with fifteen genera of Algæ (*Vaucheria*, *Hydrodictyon*, &c.) and two genera of Fungi (*Eurotium* and *Mucor*), making sure in each case that he had a pure culture to start with. His aim was to discover whether external conditions determine the occurrence of the various forms of reproduction, and what these conditions are. The factors investigated were nutrition, moisture, light, temperature, and chemical reagents; and the general result is a proof that certain external conditions determine the occurrence of asexual reproduction (by zoospores), while others as certainly evoke sexual reproduction (by gametes).

A single illustration may be given. In the case of *Vaucheria*, zoospores are always formed when filaments which have been kept moist for some days are soaked in water, or when they are removed from a very dilute nutrient solution and placed in pure water, or when those which have been growing in water or in a very dilute nutrient solution are placed in the dark. On the other hand, if the filaments are placed in a 2–4-per-cent solution of cane-sugar in bright light, sexual reproduction by gametes always occurs.

This may seem by no means extraordinary to some, but it is the *beginning* of a physiology of reproduction in plants.

Chapter VIII.

The Conditions of Life and Death.

Three Periods of Opinion—The Organism and the Inorganic World—The Quick and the Dead—Characteristics of Living Organisms—"Vital Force"—The Kinds of Death—Organic Immortality—General Conditions of Life—Origin of Life—Ancient Belief in Spontaneous Generation—Mediæval Beliefs—Redi's Experiments—Slow Death of the Theory of Spontaneous Generation—Pouchet and Pasteur—Tyndall—The Fact of Biogenesis—Opinions as to the Origin of Life upon the Earth.

Three Periods of Opinion.

All vital activity implies interaction between the living creature and its surroundings, between the organism and its environment, and the most general problems of physiology have to do with this relation.

(1.) In ancient times the relation of dependence in which an organism stands to its environment was not perceived, except in an occasional prophetic flash of insight. Nor could it be otherwise until the advance of chemistry and physics made an analysis of function possible. It was also characteristic of the old days that the contrast between the living and the not-living was made little of; for the doctrine of the spontaneous generation of even highly organized animals met with general acceptance from Aristotle to Harvey.

(2.) A second period, which we may date from the discovery of oxygen, shows the growth of a conviction that the organism is in part dependent upon its surroundings. But this conviction was inhibited by the theory of a special vital force, supposed to dominate the chemical and physical processes which occur in a living body. This theory was probably strengthened

by the growing disbelief in spontaneous generation, which dates from Redi's experiments (1626–97).

(3.) The third period, which practically dates from the establishment of the doctrine of the conservation of energy, is marked by the realization of the organism's complete dependence upon its environment, and by the disappearance of the doctrine of a special vital force. But although a conviction has grown that the living and the not-living differ in degree rather than in kind, it is confessed by those who are frank that the secret of the synthesis which is expressed in living matter or in the organism remains undiscovered.

To the careless, it may seem that nothing could be easier than to distinguish the living organism from its non-animate physical surroundings. But is there anything more difficult?

The Organism and the Inorganic World.

Are we inclined to lay emphasis on form and structure? Then we recall the exquisite beauty of some dendritic minerals and the formlessness of the amœba, the complexity of many crystals and the apparent simplicity of a slime fungus.

Or is it the power of *growth* that impresses us as characteristic of the organism? What then of the inorganic crystal which grows beautifully under our eyes? Or if it is development, the passing from stage to stage, that characterizes life, what then of the vapour that passes into the form of a snow-flake which is dissolved again into water.

Is the organism a material system, with the power of changing matter and energy from one form to another and doing work thereby? But so, in truth, is the steam-engine.

Is it the power of movement that we would emphasize as characteristic of life? What then of the fragment of potassium darting hither and thither on the surface of the water?

Is it irritability that characterizes life? But what is irritability but the power of responding to stimulus, and surely even the barrel of gunpowder will do that?

Nor is any chemical characteristic of the living organism at first sight apparent. It is certain that there is

no material element in the organism which is not to be found in the inanimate environment. It is all a question of chemical composition. The results of synthetic chemistry have broken down the supposed barrier between the organic and the inorganic.

Nor can any foothold be found in emphasizing the co-existence of psychical phenomena and life, for it is plain that we know, to say the most, very little as to psychical phenomena in the simplest animals, and nothing as to their expression in plants.

The difficulty of defining vitality remains when we contrast not the bird and the pebble, but the living bird and the corpse, the quick and the dead.

The Quick and the Dead.

Even in practice it is often difficult to tell whether an organism is alive or dead; the theoretical distinction is not less difficult. The contrast is indeed great between the soaring lark and the dead bird at our feet; but what if we contrast the corpse with the entranced fakir, or with the dried-up bear-animalcule, or rotifer, or paste-eel, or even more familiarly with the seed many years old?

As far back as 1719, Leeuwenhoek wrote to the Royal Society of London an account of the revivification of the little bear-animalcules or Tardigrada, animals distantly related to mites, which occur for instance in the gutters of house-roofs and have extraordinary powers of surviving drought. The same is true of many small Crustacea and of some rotifers or wheel-animalcules, and is perhaps most securely known in regard to the minute thread-worms (Anguillulidæ) known as paste-eels and vinegar-eels, which may "come to life again" after being dried up for fourteen years. It is less surprising that the same should be true of many eggs and spores and unicellular organisms, where the structure is much simpler.

Now it is plain that these organisms in a state of latent life, as Claude Bernard phrased it, or "potential life", as Preyer calls it, are not dead, since they may live; yet beyond this potentiality it is difficult to say what characteristic of livingness they possess.

Of interest in the same connection are the phenomena

of local life which remain in parts of an organism, *e.g.* the turtle's heart, which may beat long after the continued life of the entire animal is out of the question, indeed after the bulk of the creature has been made into soup.

In short, here again we face the suggestion that the state of life and the state of death are but the extremes of a long series.

Characteristics of Living Organisms.

From Treviranus to Verworn, from Claude Bernard to Le Dantec, biologists have endeavoured to state the characteristics of living organisms; but a historical summary is not yet justified, since so little progress has been made. It is not even possible to say that we have got rid of mysticism. We have become more concrete than Linnæus was when he penned his famous aphorism—"Lapides crescunt; vegetabilia crescunt et vivunt; animalia crescunt, vivunt, et sentiunt"; and we have probably become more aware of our ignorance.

It is not, therefore, with any confidence that we here emphasize three characteristics which distinguish the living from the not-living.

(1) The first is the power of *organic growth*, the power of repairing loss and increasing size at the expense of material more or less different from that which forms the organism. The crystal grows, but it grows only out of material *similar* to itself, while the grass grows at the expense of air, water, and salts, and the horse at the expense of the grass.

(2) The living creature, as long as it is actively alive, is interacting with its environment; it is the subject of more or less continuous chemical changes, some of which are direct reactions to the outside world, while others are only indirect reactions; yet, in spite of this flux and unrest, the organism remains for variable periods much the same, it retains its integrity or unity of character.

(3) An organism is often compared to an engine, and the two are alike in being material systems adapted for the transformation of matter and energy from one form to another. But there are differences. Not only is

the organism a self-stoking and a self-repairing engine, both notable qualities, but there is an even deeper contrast, which has been stated by Dr. Joly in a remarkable paper entitled "The Abundance of Life" (*Proc. Roy. Dublin Soc.*, 1890): "While the transfer of energy into any inanimate material system is attended by effects retardative to the transfer and conducive to dissipation, the transfer of energy into any animate material system is attended by effects conducive to the transfer and retardative of dissipation". Following probably from this we have the great contrast, which admits of no denial, that however perfect the inanimate engine may be in its work and longevity, it never gives rise to other engines, while it is characteristic of the organism that it is reproductive.

"Vital Force."

Over and over again in the history of biology the doctrine of a special vital force has arisen, held sway for a time, and then disappeared. It arises as a reaction from the false simplicity of premature solutions, or as a despairing retreat in the face of baffling problems, or as the result of misunderstanding the real aim of science.

The doctrine is an old one, for even if we ignore the speculations of the ancients, it must date at least from Paracelsus and Van Helmont. As it has naturally taken very different forms in different generations, the word "vitalism", so often used, has little definite meaning. There is a sense in which no modern physiologist is a vitalist, since none rejects physico-chemical interpretations as the early French vitalists did; there is a sense in which all modern physiologists are vitalists, since none pretends to know the secret of that particular synthesis which even the simplest of organisms illustrates.

The phrase "vital force" may be used as a general expression for the energies resident in living matter, and may serve to suggest that we do not at present understand them, or how they are related in the unity of the organism. But the phrase was originally used to denote a "hyper-mechanical force", a mystical power, resident in living creatures, and quite different

from thermic, electric, and other forms of energy. This was the meaning attached to the phrase by the disciples of Haller, by Louis Dumas (1765–1813), by Reil (1759–1813), and the other early vitalists. It can only be said that an appeal to such a force violates the scientific method, and abandons the scientific problem. Again and again, in regard to particular points, subsequent progress has shown that the loss of faith in science was premature.

According to the hypothesis of vitalism the phenomena of life are inexplicable apart from a special vital force exclusively resident in organisms, and different from the chemico-physical energies of the inanimate world. Thus the great pathologist and anatomist Henle (d. 1885) believed in a non-material agent associated with the organism, "presiding over the metabolism of the body, capable of reproducing the typical form, and of endless partition without diminution of intensity".

It is altogether an error to suppose that a refusal to believe in such a special "vital force" implies materialism. The questions are quite separate; the former has to do with scientific method, the latter is a philosophical theory. Thus Huxley was certainly no believer in "a vital force", yet he was clearly an idealist; and the same might be said of many.

Every physiologist will, I believe, admit that he cannot at present give a physico-chemical interpretation of contractility or of irritability, of digestion or of absorption, of respiration or of circulation. What he can give is a partial analysis of these functions in simpler terms. This must remain the case until we discover the secret of the synthesis which the simplest unicellular organism expresses. In regard to some points the translation of vital functions into physico-chemical processes seems further off than it did twenty years ago, but that is because we are less readily satisfied.

The "neo-vitalists", such as Bunge and Rindfleisch, emphasize the fact that there is no present possibility of giving a complete chemico-physical restatement of any observed function; that there are always residual

phenomena; and that the known physico-chemical causes do not seem adequate to the result. In other words, the categories of mechanism, of chemistry, and physics, cannot be forced upon vitality without doing violence to the very idea of the organism—a complex adaptive synthesis of matter and energy whose secret remains unread.

When the neo-vitalists go further, and insist on an idealist as opposed to a materialistic conception, they may be quite correct, but they are raising another question, which is philosophical rather than biological.

The Kinds of Death.

Biologists are so often preoccupied with anatomy, and the analysis of the dead, that critics have scoffed at biological work as "mere necrology". The criticism is healthful, for it must be a purblind biology that ignores the intact living creature; yet in justice it must be remarked that anatomical analysis has done much to vitalize our conceptions of the living. There is a real sense in which it is true that it is only by knowing the dry bones that we can ever really see a living bird. Indeed, one of the characteristic advances of modern biology is a clearer understanding of death. When we understand death much better, we shall understand life a little.

Death plainly means the irrecoverable cessation of organic life, but it seems profitable, both theoretically and practically, to distinguish (*a*) violent, (*b*) microbic, and (*c*) natural death.

(*a*) Violent death, like that of the grouse shot by the sportsman, of the worm swallowed by the fish, of the jelly-fish stranded on the beach, is clearly separable from other forms of death. Life is a function of organism and environment; a violent change in either term of the function spells death. Although there are some organisms, perhaps all fishes, which always die a violent death, it seems fair to regard violent death as something catastrophic, accidental, or casual, something extrinsic and not inevitable.

(*b*) Distinguishable from violent death, connecting it with natural death, is what we may call microbic death, which bulks largely in the mortality of organisms. We

mean that form of death which is brought about by the intrusion of bacteria. Poisoning the system with their waste products, choking the blood-vessels, causing fatal lesions, setting up inflammation—in many ways these intruders cause death, which can hardly be laid to the fault of the organism except in so far as its powers of resistance are imperfect.

(*c*) Natural death is that cessation of life which results from the accumulation of physiological arrears. Day after day, year after year, it may be decade after decade, the machinery of the living body holds out; its necessary wear and tear is made good again by food and in rest, but the recuperation is not always complete. Especially if there has been over-stimulation, as in the case of brain-cells, or over-strain, as in the case of the heart, there is a slow mounting up of physiological debts. In fact the living organism, unless it be a very simple one, goes slowly into debt to itself. The items may be infinitesimal, but the sum-total involves that physiological bankruptcy which is death.

In contrast, then, to the old view that natural death is an intrinsic necessity, the modern conception, as worked out by Weismann and others, regards death as incident on the complex organization of the body, on the limits which are set to the asexual multiplication of cells, and on the occurrence of expensive processes of reproduction. Moreover, Weismann has argued that the length of life has been, must have been, affected by the action of natural selection. "Worn-out individuals are not only valueless to the species, but they are even harmful, for they take the place of those which are sound. Hence, by the operation of natural selection, the life of our hypothetically immortal individual would be shortened by the amount which was useless to the species. It would be reduced to a length which would afford the most favourable conditions for the existence of as large a number as possible of vigorous individuals at the same time."

Organic Immortality.

Thoughts of death lead on naturally to thoughts of immortality, on which, in a limited sense, the biologist has something to say.

It was Weismann, with his characteristic habit of

pushing ideas to their logical limits, who startled biologists by the conception of the immortality of the simplest organisms—the unicellular Protozoa and Protophytes.

It is not difficult to see that these cannot be subject to death in the same degree as higher animals are.

(1) In the first place, being single cells, without any "body", they are able to sustain the equation between waste and repair for an indefinitely long period. It is conceivable that some of the simplest may have been living on since life began. They make good their waste by continuous and perfect repair. This has been summed up in the epigram that death was the price paid for a body.

(2) In the second place, it is a well-known fact that among multicellular organisms reproduction is attended with loss of life. One of the simplest—an Orthonectid—dies in giving birth, and the same is true of some worms. Death follows close on the heels of reproduction in the case of animals so different as may-flies, butterflies, and lampreys. Everyone knows that flowering and fruiting exhaust the energies of annual plants. In the very morning of life immortality was pawned for love.

In the Protozoa and Protophytes, however, where the distinction between "body" and reproductive elements has not been differentiated, reproduction is a simpler, less expensive process. The Amœba divides into two, only a metaphysical individuality is lost. There is as little death as when two cells fuse into one, another familiar reproductive phenomenon. Similarly, with spore-formation and budding, we cannot speak of death when there is nothing—not even ashes—left to bury. More prosaically it may be said that the conception of natural death which applies to the multicellular organisms does not apply in the same degree to those which are unicellular.

Maupas has indeed pointed out that an isolated family of Infusorians, all descended by asexual multiplication from one cell, and therefore not coupling or conjugating with one another, will, after a certain number of genera-

tions, come to extinction. But this isolation is hardly a natural condition, and was not included in Weismann's doctrine. Nor, of course, does he deny the violent death of Protozoa.

(3) Thirdly, it is worthy of note that at least many Protozoa are not subject to death from bacterial infection to the same degree as higher animals. The Amœba, for instance, seems but little perturbed by the presence of various virulent microbes. It engulfs them and digests them, as the phagocytes of higher animals do when in vigorous health, or when the odds against them are not too strong.

Assuming, then, that the simplest organisms are not subject to death in the same degree as higher animals are, what of immortality in the latter?

The only biological contribution to this question, which has of course nothing whatever to do with the religious conviction of spiritual immortality, is the doctrine of the organic continuity of the germ-cells or germ-plasm, which many have spoken of as immortal.

Weismann has made this conception most precise, but it has been in the minds of many. Goebel quotes this fine expression of it from Sachs: "That which has maintained itself alive, and has continually reproduced itself since the beginning of organic life upon the earth, moving steadily onward in the eternal change of all structures, in the unvarying alternation of life and death, *that* is the embryonic matter of vegetation, and it is this which in certain cases differentiates itself into the two sexes in order again to unite".

General Conditions of Life.

The forms of life are so varied that there is almost no corner of the earth or sea where it would be safe to predict the absence of organisms. On the mountain top and the floor of the deep sea, on the polar snow and in the desert sand, in the Mammoth Cave and in the Great Salt Lake, in the hot spring and in the polar water, almost everywhere we find life. It might, perhaps, be called a modern achievement, the demonstration of the almost universal distribution of organisms upon the earth, and the recognition of that protean plasticity which enables

organisms to adapt themselves to conditions which often seem to us most unpropitious.

As living implies expenditure of energy, an income of food is obviously essential to continued activity; and yet we know that even food can be done without for prolonged periods. Succi fasted for thirty days, and the salmon seems to eat nothing for many months. Some slow-going animals, like Amphibia, are said to be able to fast for years, and there is no doubt of this in the case of organisms which pass readily into the state of latent life.

Water is another essential, but again the limits of necessity are wide. The desert plant, the spore in the air, the dry seed, the encysted Protozoon, the desiccated wheel-animalcule and water-bear, show that although water is necessary to keep the wheels of life going, it may be in great part removed without irretrievably spoiling the mechanism.

Since Priestley discovered oxygen and Mayow compared living to slow combustion, it has been recognized that an essential step in metabolism is the oxidation of carbon compounds. Yet here again the necessity for careful statement soon becomes obvious, and we learn once more the lesson, that life does not readily admit of being bound up in formulæ. Pasteur and others showed the existence of "anaërobic" micro-organisms, which are able to live and flourish in media containing no free oxygen, as the yeast-plant familiarly does in the brewer's vat, the solution of the riddle being simply that these "anaërobics" obtain the oxygen they require by splitting up the complex substances amid which they live. Similarly, Bunge has shown that parasitic thread-worms which live in the food-canals of many animals may be quite lively for 4–5 days in media entirely free from oxygen. As their store becomes exhausted, however, they sink into latent life.

For most of the higher plants and animals the limits of temperature consistent with life are comparatively narrow, but this is far from being the case with all. Over and over again, earth-worms, fishes, and frogs, not to speak of simpler creatures, have been thawed out

of hard ice, and survived. And although it is usually said that a temperature a little below freezing point, say -4° C., inside the body of an organism certainly means death, Raoul Pictet, who has had much experience with low temperatures, found that frogs might survive -28° C., snails -120° C., and bacteria -200° C.

About 47° C. is usually mentioned as the temperature which infallibly kills the living matter of ordinary plant-cells in water, and less is usually sufficient to kill small animals in water; yet there are hot springs in which both plants and animals flourish at about 50° C., and the spores of the anthrax bacillus are able to survive exposure to over 100° C.

Similarly, there are limits of pressure to be considered; but we need not go further. From our present historical point of view we have only to notice that much interesting experimental work has been done in recent years in determining the limits of vitality in relation to such essentials as food, moisture, oxygen, heat, and pressure, the general result being to intensify our impression of the plasticity of life.

Origin of Life.

If it were the object of this book to give a statement of the established facts of biology, our discussion of the origin of life might be condensed into a single sentence: we do not *know* anything in regard to the origin of life. The only certainty is a negative one—there is no established case in which living organisms have arisen apart from parent organisms of the same kind. But as the whole aim of the book is historical, and as the problem of the origin of life has bulked largely in the history of biology—much more largely in the past than it does now; and as, moreover, the biology of the Victorian Era claims to have finally dismissed, not the possibility of, but all pretended instances of spontaneous generation, it seems in keeping with our purpose to devote a few pages to some account of the long-drawn-out discussion.

If the longevity of a belief were an index to its truth, the theory of spontaneous generation should rank high among the veracities, for it flourished throughout twenty centuries and more. We cannot trace the history of

the theory in all its details, but the story may be recommended to the psychological historian as a labyrinth of error, with glimpses of truth at every turn.

Ancient Belief in Spontaneous Generation.

Even Aristotle (384–322 B.C.), the founder of Biology, believed in spontaneous generation, but he did not accept the current creed lightly. In point of fact he devoted no small space, and no little ingenuity, to its discussion. Thus it was almost exclusively in regard to invertebrate animals that Aristotle postulated spontaneous generation; except in the case of a few fishes, such as eels (whose generation was till very lately a complete puzzle), he held that vertebrates arose as the result of pairing. As to insects and the like, Aristotle was well aware that they were male and female and reproduced sexually; he was even aware of the partial parthenogenesis of bees' eggs, those which become drones having a mother but no father: what he asserted was, that spontaneous generation occurred as well. He seems to have been especially and naturally puzzled by the sudden appearance of internal parasites, and by the occurrence of small animals in putrefying substances—facts which were not explained until quite modern times.

From Aristotle to Augustine, from Lucretius to Luther, on through the long centuries the belief in spontaneous generation remained unshaken.

Mediæval Beliefs.

Even a man like Cesalpino, who did some excellent botanical work, and had, long before Harvey, some clear ideas as to the circulation of the blood, believed that frogs might be generated from the mud with the help of sunshine, and even suggested a similar origin of the aboriginal Americans. The botanists were no better than the zoologists. One of their favourite notions was that the green dust which grows in damp weather on trees and stones, which is now known to consist of unicellular Algæ, such as *Pleurococcus*, was a standing evidence of the genetic connection between the dead and the living, between the mineral and the vegetable; even Bacon of Verulam believed in the spontaneous origin of some higher plants, like thistles, from dead earth; and the Italian botanist Matthioli

regarded the duckweed (*Lemna*), whose leaf-like shoots are so common on the surface of pools, as a condensation of the still water, and a starting-point for higher forms of plant life.

While even Harvey continued to believe in spontaneous generation, the scientific attitude in relation to this problem was at last represented by his Florentine contemporary, Francisco Redi (1626–97), distinguished alike as scholar, poet, physician, and naturalist. By a few simple experiments he did much to shatter the dogma of spontaneous generation, and to establish the conclusion *omne vivum e vivo*. In their own way these experiments are comparable to those of Tyndall and Pasteur two hundred years later. He showed that, if the flesh of a dead animal was protected with sufficient care from intruding insects, no grubs or insects developed in it. It was, indeed, a simple experiment, but no one had made it before! Redi also tackled the problem of the origin of parasites, but the cases he took were difficult, *e.g.* the maggots inside a sheep's skull, and he did little beyond raising the question. He was also baffled by the occurrence of young insects within galls, and seems almost, in spite of himself, to have been forced to conclude that the galls produced the insects.

Redi's Experiments.

We have already noticed that the origin of internal parasites puzzled Aristotle, and it was long before any solution was arrived at. To some it seemed enough to suppose that they arose spontaneously from the juices of their host; to others it seemed clearer to say that they were created along with the host in the beginning, and were handed on as part of the inheritance from generation to generation. Thus Adam was said to have contained all the human parasites from the first,—a state hardly consistent with Edenic bliss. The sagacious Leeuwenhoek (1632–1723) was one of the first to insist that all the internal parasites of man and animals came from outside, either as such or as germs, but he did not prove his case. In fact, there was only one way of proving it, namely, by experiment, but that was not achieved until the nineteenth century, through the

careful work of Von Siebold, Leuckart, Küchenmeister, Van Beneden, and others. The working out of the life-history of the common tape-worms or of the liver-fluke are familiar cases in point.

Slow Death of the Theory of Spontaneous Generation.

Aristotle had excepted the higher animals from the possibility of spontaneous generation, Redi had destroyed the supposed case for insects in carcasses, even the spontaneous origin of endoparasites was becoming doubtful; in short, the flimsy evidence began to crumble away. This was partly due to the development of criticism, partly to the work of the early microscopists and anatomists, who showed how complex most of the lower animals are; and partly perhaps to a growing sense of the physiological gulf between the living and the not-living.

But Redi's experiments were held to controvert the Scriptures, and we find the Scotch priest Turbervill Needham trying hard (1750) to give experimental proof of the spontaneous origin of wheat-eels (small Nematode worms),—an attempt which Voltaire derided with bitter sarcasm. But no experimenter is to be despised, and Needham did good service in directing attention to a weak point in the case against spontaneous generation. He showed that animalcules (Infusorians and the like) appeared even in decoctions which had been boiled and corked up. As we should now say, this result was due to imperfect sterilization and imperfect corking of the tubes; but it was used by Buffon, who was much interested in Needham's work, to bolster up a pet theory of his, that life resided in indestructible organic molecules, and that these were liberated after death or in decomposition as the aforesaid Infusorians or animalcules.

On the other hand, the Abbé Spallanzani (1729–99), who made many interesting though often careless and ruthless experiments, criticised Needham's researches, and anticipated the modern practice of sterilization by showing that even minute forms of life did not develop in decoctions which had been *well* boiled and then hermetically closed up.

After Spallanzani's experiments the discussion took another turn. It was objected by the chemists, who had now discovered oxygen, that life could not be expected where this gas was more or less absent, and that the boiling process might irretrievably injure the "organic molecules". Schultze and Schwann (1836, 1837) were thus led to make fresh experiments; they carefully boiled the infusions and supplied air which had been passed through red-hot tubes,—no animalcules appeared; they then supplied air which had not been so purified, and in the same infusions the animalcules appeared. This was improved upon by Schrœder and Dusch (1854–59), who did what we now so often do as a class experiment: they boiled infusions, and while the steam was coming off plugged the neck of the flask with cotton-wool. This allows the passage of oxygen, but keeps back germs; and in most cases the sterilization is quite effective. Meanwhile Schwann and Cagniard de la Tour had been working towards the conclusion for which Pasteur did so much to win conviction, that all putrefaction and many kinds of fermentation are due to the activity of minute living organisms. Thus the discussion narrowed till there was, it might have seemed, no debatable point left.

Pouchet and Pasteur.

But error dies hard, and in 1859 Pouchet published his *Hétérogénie*, in which almost all that could be said in favour of spontaneous generation was again said. In 1858 he had claimed before the Academy of Sciences that he had succeeded in proving the origin of microscopic organisms apart from pre-existing germs. The historical interest of Pouchet's work in this connection is simply that it provoked Pasteur, against the advice of his friends, to some of his fine work. Pasteur knew more than Pouchet as to the insidious ways of microbes; he showed the weak point of his antagonist's experiments, and gained the prize offered in 1860 by the Academy, for "well-contrived experiments to throw new light upon the question of spontaneous generation". Pasteur threw light on the subject by his study of the organized particles—many of them living or dead bacteria—which float in the air.

He opened twenty sealed flasks containing organic infusions in the pure air of the Mer de Glace, and only one thereafter showed signs of life; but eight out of twenty opened on the plains, and all of the twenty opened in town, developed germs. By these and other experiments, which are commonplace already—*e.g.* finding the germs which were caught in the cotton wool filters, and proving that they developed when placed in suitable solutions—he was led to his brusque conclusion that "spontaneous generation is a chimera", which, as a statement of fact, is true.

Tyndall.

Although the great achievements of Tyndall (1820–93) were in physical, not biological research, his work in connection with spontaneous generation must always have honourable mention. As early as 1869 he had made ingenious experiments in regard to the particles which float in the air, and for some years afterwards he continued to apply the exact methods of experimental physics to the question, "Can air, retaining all its gaseous mixtures, but cleaned from mechanically suspended matter, produce putrefaction?" The result was to show that when dust was present, rotting occurred in the exposed infusions; when dust was absent, there was no rotting.

In the course of his experiments Tyndall made the important discovery, which has been recognized by all bacteriologists, that to secure absolute sterility in infusions it is safer to have an *intermittent* application of heat. In other words, what a single boiling may not ensure, since the spores of some bacteria are much more resistant than the full-grown cells, is certainly effected by subjection to high temperature on three consecutive days.

In concluding his experiments, Tyndall said, with justifiable confidence: "There seems no flaw in this reasoning; and it is so simple as to render it unlikely that the notion of bacterial life developed from dead dust can ever again gain currency among the members of a great scientific profession".

In his presidential address to the British Association in 1870 Huxley declared his conviction that the fact of

biogenesis, that life arises from pre-existing life, was thoroughly established. At the same time, he expressed his *opinion* that if he could have been a witness of the beginning of organic evolution he would have seen the origin of protoplasm from not-living matter. The point is clear; on the one hand, the biologist makes the negative statement that so far as he is aware no form of life has ever been observed to arise except from a parent form of the same kind; on the other hand, he suggests the limitation that there may have been, or may still be, conditions in which not-living matter acquired the potentialities which we call life.

The Fact of Biogenesis.

The conclusion, then, which most modern biologists accept is, that while there is no known evidence of not-living matter giving origin to living organisms, this does not necessarily exclude (*a*) the possibility that this once took place, (*b*) the possibility that it is taking place now, or (*c*) the possibility that it may be made to take place again. If any of these possibilities should express realities, then our estimate of the potentialities of not-living matter must be heightened. It should perhaps be noticed, as a sagacious friend has pointed out to me, that protoplasm or living matter may still be forming "in extremely small quantities, too small to be visible, and of simple or no structure, but yet sufficiently complex in composition to serve as food for organisms". It goes without saying, however, that possibilities do not enter into the solid framework of science.

Since our data are practically nil, the scientific attitude in regard to the problem of the origin of life must be agnostic. Yet many opinions on the subject have been ventured, and some of them are both interesting and stimulating.

Opinions as to Origin of Life upon the Earth.

Quite different from the others is that of Alfred Russel Wallace, who postulates a spiritual influx at the origin of life and in connection with some other great events of history.

In 1865 and afterwards H. E. Richter expounded his hypothesis that living germs might be eternal, *omne vivum ab æternitate e cellula*, and that they might drift through space from sphere to sphere, lodging and de-

veloping where the conditions were favourable. Helmholtz also asked whether the question as to the origin of life was not as ultimate as the question as to the origin of matter, and lent his authority to the hypothesis that germs of life might have reached the earth from other spheres. But the best-known name in this connection is that of Lord Kelvin, who did not see any serious improbability against the theory that life was borne to the earth by meteorites. This would, so to speak, shift the responsibility of the problem off the earth, leaving the solution *elsewhere*.

The bold conception suggested by Richter and Helmholtz was further elaborated by Prof. W. Preyer. Far from supposing that the inorganic might have given rise to the organic, he asked whether the dead was not as probably the product of the living. And everyone knows that many rocks could not have been as they are apart from life. Even in the times when the earth was a fire-ball there may have been, Preyer supposed, molecular combinations which bore in their inter-relations the secret of life, of life very different from that in any form which we know, but still of life. It is doubtful, however, whether this hypothetical extension of the conception of vitality can serve any useful purpose.

The *opinion* towards which the majority seem to swing round is that which was expressed with great clearness by Hæckel in 1866, that analogy points to an erstwhile origin of living matter from not-living matter. The botanist C. von Nägeli, the zoologist Ray Lankester, the physiologist Pflüger, may be mentioned as prominent workers who have more or less fully accepted Hæckel's position.

We cannot close this chapter without recalling the now familiar fact that the discussion is not a merely theoretical one, but has been unusually rich in practical results. It led on to discoveries in the preservation of food and the improvement of food-products, to an entirely new view of parasites, to the use of antiseptics, and to the cure of many diseases.

Chapter IX.

Cell and Protoplasm.

The Early Microscopists—Bichat's Step—The Cell-theory—Corroboration of the Cell-theory—Criticism of the Cell-theory—Modern Analysis of the Cell—Cell-division—The Cell-cycle—Structure of the Cell-substance—Protoplasm—Anabolism and Katabolism—Conception of Ultimate Vital Organization.

The Early Microscopists.

Harvey made his minuter observations with the aid of a simple lens such as every field-botanist now carries in his pocket, and one must admit that without some better instrument the analysis of structure could not have advanced far beyond what Harvey achieved. The better instrument, which opened up a new world, was the compound microscope, invented about 1600 by Hans and Zacharias Jansen, and rapidly improved by other workers. In the seventeenth century it was used to good purpose by a number of enthusiastic observers who revealed minutiæ of structure hitherto unsuspected. Malpighi in Italy, Leeuwenhoek and Swammerdam in Holland, Hook and Grew in England, were among the most notable of these early histologists.

Bichat's Step.

When we consult the works of the early microscopists we cannot help feeling that they often played with their new scientific toy, just as we often play with stains and microtomes. They magnified without purpose, and accumulated descriptions and figures of what are called "interesting objects" or "microscopic curiosities". The play-period in science as well as in life may be essential as an apprenticeship to serious work; but it must be allowed that there is no direct gain in magnifying an object a thousand times, or staining it with three colours, *unless* the magnifying and the staining help us to understand the object better, or keep us from misunderstanding it.

Without any depreciation of the keen vision of Leeuwenhoek or Swammerdam and their contemporaries,

which would be an impertinence, we cannot deny that it was long before their work led to any new general idea; all that can be said is that they revealed a new world of detail which both physiologist and embryologist had to take account of, and which in a few cases helped to deepen physiological and embryological understanding.

The first generalization of importance was within the nineteenth century, namely Bichat's analysis of the organism into a series of *tissues* with definite structural characters—nervous, muscular, connective, glandular, &c. We now define a tissue as an aggregate of more or less uniform cells or modifications of cells, but this definition implies a step of analysis beyond Bichat's. The step he took was really this—the anatomist had disclosed organs, such as heart and lungs; Bichat analysed these organs into their component tissues (muscular, connective, nervous, &c.), and also endeavoured to show that the function of the organ was expressible in terms of the properties of these tissues.

Very gradually, by numerous isolated observations, an approach was made towards laying that foundation-stone of modern biology which is usually spoken of as the cell-theory.

The Cell-theory.

In 1838 Schleiden showed that plants were built up of cells and modifications of cells, and discovered the origin of the plant-embryo to be a single cell or ovum. In the following year Schwann extended these two observations to animals, and thus the "cell-theory" was formulated. "No other biological generalization," says Prof. Wilson, "save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view, or has accomplished more for the unification of knowledge."

The cell-doctrine in its full statement includes three propositions: the first morphological, the second embryological, the third physiological.

(1) *Morphological.* All organisms are either single corpuscles of living matter (the unicellular Protozoa, Protophytes, and Protists) or are built up of a large number of such corpuscles and modifications of these

(Metazoa and Metaphyta). In short, all plants and animals have a cellular structure.

(2) *Embryological.* Every organism, reproduced in the ordinary way, begins its life as a single cell. The simplest organisms rarely get beyond this stage; almost all remain strictly unicellular. But in all other cases the original single cell in which the individual life begins —the fertilized ovum—divides and redivides into a coherent mass of cells, and gradually gives rise to a more or less complex body.

(3) *Physiological.* The functions of a multicellular organism are expressible in terms of the activities of its component cells. "Each cell", Schleiden said, "leads a double life: an independent one, pertaining to its own development alone; and another incidental, in so far as it has become an integral part of a plant" (1838). "The whole organism", Schwann said, "subsists only by means of the reciprocal action of the single elementary parts" (1839). "Every animal", Virchow said, "appears as a sum of vital units, each one of which bears with it the characteristics of life" (1858).

These three conclusions combine in impressing us with the unity of organic nature, for although a plant-cell is often very different from an animal-cell, and one animal- or vegetable-cell may be very different from another in the same or in another body, yet the points of agreement in structure, in development, and in function are at least as striking as the observable differences, and often more striking.

Corroboration of the Cell-theory.

Before the cell-theory could attain to the dominant influence which it has exerted for half a century on biology, it required to be corroborated in various directions.

It had been recognized that the ovum was a single cell, and the spermatozoon likewise; as early as 1824 Prevost and Dumas had studied the cleavage of the fertilized ovum; it remained to follow the segmentation-cells on to their final differentiation into tissues. At early dates strong steps on this line of research were taken by Reichert (1840), Henle (1841), Remak (1841-1852), and Kölliker (1843–1846).

Probably all living histologists would agree that the veteran of their craft, of whom they are proudest, is Professor Albrecht von Kölliker. The magnitude of his work, alike in quantity and quality, is a lasting example to the spirit of research. He helped in establishing the cell-theory, he traced the origin of tissues from the segmenting ovum through the developing embryo, he demonstrated the continuity between nerve-fibres and nerve-cells of vertebrates (1845), he isolated the elements of smooth muscle (1848), he did lasting work in connection with the development of the skull and the backbone (1849–1850), and much more, all in the early years of his scientific activity. Since 1850 hardly a year has passed without some important histological, embryological, or anatomical work from Von Kölliker, as may be readily verified by turning up the famous *Zeitschrift für wissenschaftliche Zoologie*, which was founded by him and Von Siebold in 1848.

On the physiological side it was necessary to show in greater detail that the life of the body was to some extent expressible in terms of the internal changes in the constituent cells. Epoch-making in this connection was the work of Goodsir (1845), and Virchow (1858), who demonstrated that both in normal and pathological processes cells arise from pre-existing cells, and that the life of the whole may be spelt out in the life of the parts.

Criticism of the Cell-theory.

While most naturalists believe strongly in the structural, functional, and developmental importance of cells, there have been frequent protests against regarding the cellular standpoint as ultimate.

(*a*) *Morphological Criticism.* That development proceeds by cell-formation is a cardinal part of the cell-doctrine. But it has been pointed out, by Sedgwick (1894) in particular, that in some cases, *e.g.* the development of a species of *Peripatus*, the nuclei divide without corresponding cell-divisions, and the result is a "syncytium" or protoplasmic mass with many nuclei, but with undefined cell-boundaries.

(*b*) *Physiological Criticism.* That the organism lives

in virtue of the reciprocal action of its component cells is another fundamental conclusion of the cell-doctrine. But it is evident that there can be no physiological resting-place here, since metabolism is a chemical process, and must be so expressed in the long run. The life of the city is not intelligible in terms of the houses merely; we must analyse down to the members of each household.

(*c*) *Embryological Criticism.* More serious perhaps than either of the foregoing is the reaction from the suggestion that development is to be explained in terms of cell-formation. Thus Sachs says, "cell-formation is a phenomenon very general, it is true, in organic life, but still only of secondary importance; at all events, it is merely one of the numerous expressions of the formative forces which reside in all matter, in the highest degree, however, in organic substance". On the zoological side Mr. Sedgwick has forcibly expressed the same view.

"As far as plants are concerned", Prof. Wilson (1896, p. 293) says, "it has been conclusively shown by Hofmeister, De Bary, and Sachs, that *the growth of the mass is the primary factor*; for the characteristic mode of growth is often shown by the growing mass before it splits up into cells, and the form of cell-division adapts itself to that of the mass: *Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen* (De Bary)."

It may be doubted whether the pendulum of opinion has not been extreme in its reaction from the "cell-standpoint". From the historical point of view, it seems certain that the cell-doctrine has done more for biology than any other generalization, except that of evolution. It may have suggested some erroneous notions, as other generalizations have, but there remains a solid basis of fact, which may be re-interpreted, but cannot be gainsaid.

Modern Analysis of the Cell.

Of recent years the study of the cell, "cytology" as it is called, has indeed come in as a flood, for almost every week has seen the publication of some fairly important paper, and at times it seems difficult to find firm foothold from which to face

the tide of research and the spray of controversy. The little word cell, one of the least fortunate of scientific terms, which once seemed to express a simple fact, has now to cover a perplexingly intricate microcosm. We cannot do more here than make an outline-map of the territory.

The cell is a structural unit or unit-area,—a unified living corpuscle of complex substances. Within this unit it is convenient to distinguish certain parts. (*a*) The general cell-substance or cytoplasm has a complex structure, and consists in part of living matter (protoplasm), in part of obviously lifeless inclusions (metaplasm). (*b*) Within the cytoplasm is the nucleus, again a little world, with readily stainable chromatin substances, and illusive unstainable achromatin. (*c*) In at least a large number of animal cells, especially when they are about to divide, two small bodies known as centrosomes are demonstrable, each surrounded by a sort of halo of delicate rays—the astrosphere. (*d*) In most plant cells there is a very definite cell-wall round each unit, and this is often traversed by distinct intercellular bridges of protoplasm which link cell to cell. In the animal cell the wall is usually much less definite, but the intercellular bridges are very common.

Cell-division.

Only a few cells grow to a relatively large size, such as the giant Gregarine, parasitic in the Lobster, which may measure three quarters of an inch in length. Such cases are rare, and most cells remain microscopic. The process of cell-division is thus of fundamental interest, since it is the general mode of organic growth. By absorbing food and water a cell increases in size, and thus contributes to the increased size of the organism, but the cell's increase has usually narrow limits, therefore the growth of the organism necessitates cell-division. The brain of man and higher animals is a noteworthy exception, inasmuch as the nerve-cells do not divide after birth (except in very rare cases of injury).

There are two chief modes of cell-division, technically known as direct and indirect, or amitotic and mitotic. The former is much the less frequent, and much the less

complex. It is usually marked by the somewhat dumb-bell-like constriction of the nucleus as a whole; without complex preliminaries or manœuvres, one cell becomes two. In the great majority of cases it seems to be a secondary process, and it certainly is not the usual mode of cell-multiplication. In the usual mitotic process there is an intricate interaction between nucleus and cell-substance, and a complex co-operation of the different members of the "cell-firm",—the centrosomes, the chromosomes, the achromatin, and the general cell-substance. One might compare it to the legal complexities observable in the dissolution of partnership in an old-established firm of several members with somewhat ravelled interests.

According to Wilson's recent summary, in which he seeks to strike a balance-sheet of many opinions and observations, the centrosome is the organ of division *par excellence*, "under its influence, in some unknown manner, is organized the astral system, which is the immediate instrument of division", its rays becoming associated with the chromosomes, which are certainly of great importance, if they are not so exclusively essential as some would make out. "Mitosis is due to the co-ordinate play of an extremely complex system of forces which are as yet scarcely comprehended." Its end, however, is clear; it is "*to divide every part of the chromatin of the mother-cells equally between the daughter-cells*". There are many peculiarities in different cases; there seem to be even individual variations; there are certainly abnormalities here and there; but in plant and animal there is a fundamental similarity both of process and result.

The central corpuscles in animal cells *seem* to act as if they were centres of force, and the indescribably fine threads which pass from around them to the chromatin bodies and elsewhere have been credited with motive powers. But the cell-divisions in higher plants seem to be accomplished without the presence of centrosomes. The whole subject is beset with uncertainties. At the same time, it can hardly be doubted that such suggestions as Heidenhain's "tension-law" hold out some

hope that even cell-division will yield to physiological analysis, that is to say, that some proximate solution will be arrived at.

A general rationale of why cell-division should take place seems to have been suggested independently by Leuckart, Spencer, and Alexander James. It is often referred to as the Leuckart-Spencer principle. Why do not cells go on growing larger and larger? why do they almost always divide at a *limit of growth* more or less definite for each kind of cell in given surroundings? The answer is as follows:—Suppose a young cell, spherical in form, to have doubled its original mass by growth, that means that there is twice as much living material to be kept alive. But the living material is fed, aerated, and purified through the cell-surface, which only increases as the square of the radius, while the mass increases as the cube. The extension of surface *must* lag behind the increase of mass. Therefore when the cell has, let us say, quadrupled its original mass, but by no means quadrupled its surface, physiological difficulties set in, the normal ratio between repair and waste, construction and disruption, is seriously disturbed. At the limit of growth, then, the cell divides, halving its mass, and gaining new surface. It is true that surface may also be increased by outflowing processes, just as that of a leaf is by the formation of many lobes; and it is true that division may occur before the limit of growth is reached, but as a general rationale, quite different from physiological analysis, the Leuckart-Spencer principle seems a useful suggestion, and it is applicable to organs and to bodies as well as to cells.

An interesting suggestion in regard to the forms and phases of cell-life is due to Prof. Patrick Geddes. It may be called the conception of a cell-cycle.

The Cell-cycle.

(1) In the life-history of one of the simplest organisms ever described—Hæckel's *Protomyxa*—there are four chapters. In one chapter, the organism is encysted and breaks up into spores. These spores escape as minute lashed (flagellate) units. As they feed, they sink into an amœboid form, like minute irregular drops of

living emulsion. Finally a number flow together to form a relatively large amœboid mass or plasmodium. A somewhat similar life-history is known in many cases, and the point is that we have here a "cell-cycle" in the life-history of an individual, *i.e.* a passage from phase to phase—amœboid, encysted, flagellate, amœboid . . . and so on. These phases are regarded as primitive reactions of the protoplasm in relation to the variations in the environment (food and other forms of energy).

(2) Among the unicellular animals, or Protozoa, there are three chief types:—the amœboid Rhizopods, the encysted Sporozoa or Gregarines, and the ciliated or flagellate Infusorians. It may be said that each of these accents one chapter in the life-cycle of the simple *Protomyxa*, and there are many cases in which, although one phase is dominant, another may occur temporarily. Thus a young Sporozoon may be amœboid, or an Amœba may become encysted in unpropitious environment.

(3) But this general classification of the Protozoa into three main sets, which becomes more intelligible in the light of Protomyxa's cell-cycle, is also harmonious with that of the cells in the higher animals. Thus the Rhizopods, with their changeful outflowing processes of living matter, are comparable to the white blood corpuscles, to phagocytes, to many young ova, and to other *amœboid* cells of Metazoa. The parasitic Gregarines or Sporozoa, which have a rind and no motile processes, may be compared to degenerate muscle-cells, to mature ova, or to other passive *encysted* cells in Metazoa. And the Infusorians, with their lashes, may be compared to the cells of *ciliated* epithelium, or to the active spermatozoa of most Metazoa. And further evidence of the cell-cycle is readily procurable, as when a ciliated cell in the trachea sinks down into amœboid form, or when an amœboid young ovum becomes encysted in becoming mature

(4) The suggestion—for it has remained little more—acquires further significance when the author points out that the three chapters plainly represent the three main functional possibilities: (*a*) the amœboid units, neither very active nor very passive, form a median compro-

mise; (*b*) the ciliated Infusorians, which are usually smaller, express a relative predominance of active expenditure; and (*c*) the encysted parasitic Sporozoa represent an extreme of sluggish passivity.

The conception is of value as an attempt to get below the final results of selection to the fundamental possibilities of form and function which supplied the raw material for adaptation.

Structure of the Cell-substance.

To the earlier observers, from Dujardin and Von Mohl to Virchow and Max Schultze, the cell-substance appeared to be a homogeneous, viscid substance, including, indeed, granules and vacuoles, but still essentially structureless.

This was a natural view with the means and methods then available. But if modern work has made anything certain, it is that the cell-substance has a complex structure essentially different from that of a homogeneous substance like white of egg. This conclusion has been arrived at partly (and most securely) by observation of living cells with highly perfected (apochromatic) lenses, partly (and less securely) by using fixing reagents which kill instantaneously, and stains which differentiate part from part.

One of the first to maintain that the cell must have a more complex structure than was usually supposed was Brücke, who, in 1861, advanced a hypothesis of minute units intermediate between the molecule and the cell, an idea which has been frequently re-expressed since that date.

From Brücke, as starting-point, we might trace, through Cienkowsky, Hanstein, and others, the gradual growth of the conviction that the physical basis of life is essentially complex in structure. It is enough, however, to note that it soon began to be recognized that the cell-substance consisted of a relatively stable framework (spongioplasm, reticulum, &c.), and a more liquid or labile ground-substance (enchylema, cytolymph, &c.). Some, like Leydig and Schäfer, maintained the greater vital importance of the ground-substance, while the majority emphasized the claims of the framework—a question still beyond solution.

The attempt to delineate the structure of the framework has led to very discrepant results, the most important of which may be briefly summarized.

(1) *Reticular Structure.* In 1864–1867 Frommann and Arnold demonstrated in a variety of cells—both animal and vegetable—the existence of a network-like structure. To name those who have described this reticulum would be to give a list of many of the most illustrious histologists.

(2) *Fibrillar Structure.* Not very different is the view, which we may particularly associate with the name of Flemming, that the structure is not so much a network as a complex coil of tangled fibrils.

(3) *Granular Structure.* There are a few histologists who agree with Altmann (1886) that the cell-substance consists of a homogeneous gelatinous matrix in which granules are embedded, the granules being the important vital units, bearing to the matrix the same sort of relation that bacteria bear to the gelatinous stuff or zooglœa in which they lie.

(4) *Emulsion Structure.* Various critics, such as Kölliker, Berthold, Fr. Schwarz, have from time to time suggested that the reticular or fibrillar structure was either a post-mortem appearance, or was simply the optical expression of a really simpler structure like that of an emulsion. This view must be especially associated with the name of Bütschli, who has tried ingenious experiments in the making of "artificial cells" from drops of fine emulsion, and has shown the close resemblance between their structure and that of cells. Bütschli's interpretation of cell-structure has been received with much favour, yet a safer position is perhaps that of those who doubt whether the structure of cells is likely to be uniform. Thus Frommann, in one of his last papers, maintained that some cells seem vacuolar, that others look as if they contained a broken-up network, but that in many a reticulum is, apart from all vacuoles, distinctly demonstrable. Wiesner, too, in a recent work suggests that the structure of protoplasm may be a network, or a framework of interwoven threads, or a vacuolar honey-comb—that it varies

not only in different organisms, but even in one and the same cell.

Protoplasm.

The term protoplasm was first used by Purkinje (1840) in reference to the formative material of animal embryos; it was taken over by Von Mohl (1846) to designate the substance within the cells of plants; and was extended by Max Schultze (1861) to the animal cell, superseding the equivalent term sarcode.

It may be briefly defined in Huxley's famous phrase as "the physical basis of life", but it is used by different authors in slightly different ways. It is often used as a morphological or topographical term for the physically complex cell-substance; it is often used as a physiological term for the whole cell-substance in so far as that is actively concerned in metabolism, that is for the cell-substance *minus* obviously lifeless inclusions, precipitates, &c.; it is often used to designate an unknown quantity—the genuinely living stuff. A fourth usage, which contrasts protoplasm and nucleus, should be abandoned in favour of the terms cytoplasm and nucleoplasm.

It is at present profitless to attempt to gain a *forced* clearness in regard to protoplasm. The lack of lucidity is not due to lack of logic, but to a scarcity of facts.

In regard to a few facts there is no doubt. Thus it is certain that the material of a cell has a complex structure, but the fact does not help us much. As Prof. Burdon Sanderson says, we must "hold to the fundamental principle that living matter acts by virtue of its structure, *provided* the term structure be used in a sense which carries it beyond the limits of anatomical investigation, *i.e.* beyond the knowledge which can be attained either by the scalpel or the microscope". It is hardly too much to say that a single experiment in "microscopic vivisection", as Prof. Gruber calls it, showing, for instance, that a unit bereft of its nucleus may move and be irritable for a time, but can neither grow nor persist, has been of more physiological moment *as yet* than all the descriptions of cytoplasmic architecture.

One general idea, however, the study of cytoplasmic

structure has suggested which is of physiological interest. The idea is, that a cell consists of a relatively stable living framework, and of a changeful content enclosed by it. Prof. Burdon Sanderson expresses it thus: "The framework is the acting part, which lives and is stable; the content is the acted-on part, which has never lived and is labile, that is, in a state of metabolism or chemical transformation". This view naturally leads those who adopt it to regard protoplasm as a sort of ferment acting on less complex material which is brought within its sphere of influence. It is the strange characteristic of a ferment that it can act on other substances without being itself affected by the changes which it produces, and that it can go on doing so continuously with a power which has no direct relation to its amount. In these respects a ferment is suggestive of what many suppose living matter to be. We may note, however, that to credit the framework with essential vitality and to regard the interstitial content as merely material is an assumption, comparable to that which exalts the chromatin of the nucleus and depreciates the achromatin.

Another certain fact is, that the functioning of cells is often demonstrably accompanied by marked changes in the physical appearance of the cell-structure. Relatively simple illustrations are furnished by glandular cells, like those of the pancreas, as described by Heidenhain and others; more difficult instances are the structural changes of nerve-cells after prolonged function, as demonstrated by Hodge, Mann, and others. There is no doubt that a considerable area in the cell is often affected by vital function, and this might be called the protoplasmic area. In such facts, at least, a basis might be found for another conception of protoplasm, that it is itself the seat of constant change, that it is constantly being unmade and remade, that it is the central term in a metabolic series. Thus Prof. Michael Foster speaks of protoplasm as if it occupied the summit of a set of chemical staircases. On the one hand, there is an ascending series of assimilative or constructive chemical steps, with each of which the material taken in as food

becomes molecularly more complex and more unstable. On the other hand, the continually recuperated protoplasm becomes active as a source of energy, and breaks down in a descending series of disruptive chemical changes ending in waste products.

Anabolism and Katabolism.

Since physiology attained to precision of statement it has been recognized that there is in life a twofold process of waste and repair, of activity and recuperation, of disruption and construction. One of the first to make this general idea more precise was De Blainville, who described vitality "as a twofold internal movement of composition and decomposition". At a later date, Claude Bernard, who may be called the pioneer of the "protoplasmic movement", distinguished "disassimilating combustion and assimilating synthesis". Of recent years various researches and speculations, especially those of Hering and of Gaskell, have led to yet more precise statements in regard to metabolism, perhaps more precise than the known facts warrant.

Generalizing from his studies on colour sensation, Hering was led to regard all life as an alternation of two kinds of activity, the one tending to storage, construction, or *assimilation* of material, the other tending to explosion, disruption, or *dissimilation.*

"Metabolism", he says, "is, physiologically speaking, the essential distinction between living and dead matter. It signifies the chemical processes in living substance, by which, on the one hand, certain products are excreted as foreign bodies, and either accumulate *in situ*, or pass out into the circulating fluids; while, on the other, there is a simultaneous intake of nutritive matters to form new constituents. This last function is known as assimilation; the first may be termed dissimilation."

"In distinguishing these functions, we must not fall into the error of regarding them as two intrinsically separate, parallel processes, and the living matter itself as a quiescent mass, used up on one side and replaced on the other. . . . Assimilation and dissimilation must rather be conceived as two closely interwoven processes, which constitute the metabolism (unknown

to us in its intrinsic nature) of the living substance, and are active in its smallest particles,—since living matter is neither permanent nor quiescent, but is in more or less constant internal motion."

"To assimilate and dissimilate is a fundamental property of living matter, engrained deeply in its nature, and these functions continue, provided the essential conditions of life are present—without assistance of external stimuli"; though such stimuli may compel the living matter to greater activity in either direction.

Similarly, Prof. Gaskell was led from his study of nervous function to the idea that life implies an alternation of two processes—one of them a running down or disruption (katabolism), the other a winding up or construction (anabolism). There are minor differences between the two views, but Gaskell's anabolism and katabolism correspond respectively to Hering's assimilation and dissimilation.

Before we leave the subject, it may be well to recall the uncertainties. We have no knowledge of the real nature of living matter; we cannot define any substance physically or chemically, and say, *this* is pure protoplasm. According to one view, protoplasm is a mixture of complex substances; according to another view it is a single substance allied to proteids; according to a third—perhaps most probable—view there is no such thing as living matter. The meaning of the last view, which may appear paradoxical, is simply that vital function may depend upon the interactions or inter-relations of a number of complex substances, none of which could by itself be called alive. Just as the secret of a firm's success may depend upon a particularly fortunate association of partners, so it may be with vitality.

"We are compelled", said Prof. E. B. Wilson in 1896, "by the most stringent evidence to admit that the ultimate basis of living matter is not a single chemical substance, but a mixture of many substances that are self-propagating without loss of their specific character."

Even at an early date biologists recognized that the behaviour of cells, especially in development, necessi-

tated the assumption of a complex organization. In his classic work, entitled *Die Elementarorganismen* (1861), Brücke first clearly contended for the necessity of this conception. "We must", he said, "ascribe to living cells, in addition to the molecular structure of the organic compounds which they contain, still another, and otherwise complicated, structure; and this is what we designate by the term organization." "We must always see in a cell a little animal body." The necessity of the assumption is simply that we cannot conceive of function apart from structure, and that the structure must be more than that of chemical complexity is shown by the perennial marvel of the chick developing from the egg. "The species", Nägeli said in 1860, "is contained in the egg of the hen as completely as in the hen, and the hen's egg differs from the frog's egg just as widely as the hen from the frog." All through the Victorian era there has been a succession of theories and phrases as to ultimate vital organization,—the "physiological units" of Spencer, the "gemmules" of Darwin, the "micellæ" of Nägeli, the "plastidules" of Hæckel and Elsberg, the "inotagmata" of Engelmann, the "pangens" of De Vries, the "plasomes" of Wiesner, the "idioblasts" of Hertwig, the "biophores" of Weismann, and the "idiosomes" of Whitman. There is no clearer expositor of the conception than Whitman, from one of whose essays the quotations in this paragraph have been borrowed. "Development, no less than other vital phenomena, is a function of organization." "A certain grade of organization is the result of heredity." "Organic unity depends on intrinsic properties no less than does molecular unity." "Organization precedes cell-formation, and regulates it." He looks forward to finding "the secret of organization, growth, development, not in cell-formation, but in the ultimate elements of living matter or 'idiosomes'." "What these idiosomes are, and how they determine organization, form, and differentiation, is the problem of problems on which we must wait for more light. All growth, assimilation, reproduction, and regeneration

Conception of Ultimate Vital Organization.

may be supposed to have their seat in these fundamental elements. They make up all living matters, are the bearers of heredity, and the real builders of the organism."

Chapter X.

Embryology.

The Scope of Embryology—Ancient Embryology—Harvey—Bonnet and the Preformationists—Wolff and Epigenesis—Von Baer—Alternation of Generations—The Influence of the Cell-theory—Nature of the Ovum—Nature of the Spermatozoon—Fertilization—Maturation—The Mode of Development—Germinal Layers—Influence of Evolution Doctrine—The Gastræa Theory—The Recapitulation Doctrine—Substitution of Organs—Experimental Embryology—Theories of Development.

The Scope of Embryology.

Embryology is the study of the early stages in development. Its problem is the making—the "becoming"—of the organism up to a vague point at which the specific characters begin to be well defined. This limit is determined rather by convenience than by logic, for embryology is really but a part of that larger study which considers a living creature in its time-relations, and is concerned with the breaking down in old age as well as with the building up in youth.

Embryological study has two main aspects: it is, on the one hand, *morphological*, describing the form and structure of the organism at successive stages from the fertilized egg to the adult; it is, on the other hand, *physiological*, seeking to disclose the immediate vital conditions which lead on from stage to stage. The first task is obviously the easier, for at any stage the developing organism may be killed, dissected, sectioned, and photographed; the second task is beset with unconquered difficulties.

This paragraph is too much like that on "the snakes of Iceland", for there was, so far as we are aware,

almost no ancient embryology. There are, indeed, records to the effect that more than two thousand years ago, in Greece, inquiring eyes bent over the chick developing within the egg, as they do still in our laboratories, but the methods of investigation were awanting, and the most elementary facts were either unperceived or misunderstood. Moreover, it must be remembered that the wide-spread belief in spontaneous generation, and the common habit of inventing metaphysical explanations of vital processes, tended to stifle embryological inquiry.

Ancient Embryology.

The one great exception was Aristotle, whose genius foresaw what Harvey more explicitly declared two thousand years afterwards. Harvey quotes a sentence from Aristotle which deserves to be remembered: "All living creatures, whether they swim, or walk, or fly, and whether they come into the world with the form of an animal or of an egg, are engendered in the same way". And one of the most scholarly of embryologists, Prof. Whitman, has said "that part of Harvey's theory which affirms that the parts of the future organism do not pre-exist as such, but make their appearance in due order of succession, and which is so often cited as the essence of epigenesis, was all clearly stated by Aristotle".

After Aristotle, the first important name in the history of embryology is that of William Harvey (1578–1657), the immortal discoverer of the circulation of the blood. Working "in the harness of Aristotle", he maintained that "all animals are in some sort produced from eggs", but the aphorism "omne vivum ex ovo", so persistently ascribed to him, was not his, nor must it be supposed for a moment that the word egg meant to Harvey what it means to us. He maintained that practically every organism begins its individual life from an apparently simple *primordium* in which "no part of the future offspring exists *de facto*, but all parts inhere *in potentia*". But since he had no conception of what we now call "genetic continuity"—which links the germ-cells of successive generations in a continuous lineage,—he was quite unable to suggest

Harvey.

anything but a metaphysical conception of development. "Not only is there", he said, "a soul or vital principle present in the vegetative part, but even before this there is inherent mind, foresight, and understanding, which, from the very commencement to the being and perfect formation of the chick, dispose and order and take up all things requisite, moulding them in the new being, with consummate art, into the form and likeness of its parents."

It was well, indeed, that it should be pointed out that development is a marvellous progressive process, in the course of which the obviously complex arises from the apparently simple, and the dissimilar or heterogeneous from the similar or homogeneous; but Harvey overshot the mark, and made development miraculous. It is a mistake, he said, to look for any "prepared matter" in the egg; but by exaggerating this he left no material basis for the inherent potentialities, and was forced to conceive of them mystically. Moreover, he was so far from understanding the egg, that he suggested that the primordium might proceed from parents, *or* arise spontaneously, *or* out of putrefaction. As Huxley points out, Harvey believed in spontaneous generation as firmly as Aristotle did. That he did great service must be freely allowed, but there has been a tendency to read the experience of the nineteenth century into some of his sentences.

Bonnet and the Preformationists.

Charles Bonnet (1720–1793) may be taken as the most thoroughgoing representative of the preformationist school, whose erroneous doctrines greatly inhibited the progress of embryological research for more than a century. He was the discoverer of the parthenogenesis of green-flies or Aphides, and made many interesting concrete observations on polypes and worms, but after the failure of his eyesight he became more exclusively a speculative thinker. He pondered over the phenomena of generation and development, and ended, strange to say, by virtually denying them both. His central idea was the "preformation" or asserted pre-existence of the organism and all its parts within the germ. Not that he supposed

the germ to be an actual miniature of the organism, though his words sometimes convey this impression, but he postulated that the germ "contained *très en petit* the elements of all the organic parts". He assumed, he says, "as a fundamental principle, that nothing is generated, and that what we call generation is but the simple development of what pre-existed under an invisible form, and more or less different from that which becomes manifest to our senses". He thus excludes all new formation or epigenesis.

To this main hypothesis two subsidiary ones were added: (*a*) the doctrine of *emboîtement*, according to which the germ contains the preformation not of one organism alone but of successive generations; and (*b*) the hypothesis of the dissemination of germs scattered throughout the organism, and capable of developing into buds, replacing lost parts, and so forth. As surely as Harvey overshot the mark in one direction, and made development magical by failing to credit the ovum with a heritage of organization, so surely did Bonnet overshoot the mark in the opposite direction, by a theory which amounts to a denial of development altogether. His greatest service was in presenting a *reductio ad absurdum* of the extreme preformationist position.

Bonnet was supported in his extraordinary "system of negations", as Whitman terms it, by the authority of the renowned physiologist Albert von Haller. The latter started as a believer in epigenesis, but was somehow led by his studies on the development of the chick to a complete confidence in the truth of preformation. A single sentence, "Es gibt kein Werden—There is no Becoming", sufficiently indicates his position.

Throughout the seventeenth and eighteenth centuries almost all embryological thinking was dominated by this preformationist creed, and many of the disciples were even cruder than their two masters, Bonnet and Haller. All development was an illusion, it was really only an unfolding (*evolutio*) of a preformed miniature. Moreover, the germ contained not only a preformation of the organism into which it was destined to grow, but of successive generations as well. Preformed minia-

ture lay within preformed miniature in ever-increasing minuteness, as if in a conjurer's box. Thus it was computed that mother Eve must have included over 200,000 millions of homunculi, or sometimes it was Adam who was made to bear this burden. For, according to one party, the ovists, *e.g.* Malpighi, it was the ovum that contained the miniature which had to be unfolded; while according to others, the animalculists, it was the sperm which contained the preformed model.

The whole chapter is a somewhat lamentable one in the history of embryology, and yet it must be noted in fairness that the preformationist doctrine had a well-concealed kernel of truth within its thick husk of error. There is a certain sense in which the whole future organism is potentially and materially implicit in the fertilized egg-cell; there is a sense in which the germ contains not only the rudiment of the adult organism, but of successive generations as well. But in neither of these senses was preformationism understood by any of its upholders, and to say that the modern preformationists are simply returning to the views of Bonnet and Haller is to misread the history.

Wolff and Epigenesis.

Caspar Friedrich Wolff (1733–1794) was the first to raise a strong protest, not only against the doctrines of the preformationists, but against their method of speculating rather than observing. At the age of twenty-six he published his doctorial thesis, *Theoria Generationis* (1759), an embryological classic. Appealing to facts, he showed that there was, in the early stages of the chick's development, no visible hint of a preformed miniature, but that the various organs made their appearance successively and gradually, and *were to be seen being formed.* He was clear that what he saw was a development, a real becoming, a gradual differentiation from apparent simplicity to obvious complexity. And as to this all are now agreed; it is a fact of observation.

Theory and difference of opinion begin when we ask how the gradual differentiation of an apparently simple germ or rudiment is to be interpreted; and here, Wolff was in no better position than his predecessors. As

Whitman says, "Aristotle, Harvey, Wolff, and Blumenbach all traversed the same problem, and landed in the same pitfall. They all faced the question of preformation, and discovering no natural way by which the germ could come ready-made, they insisted that the germ must start anew every time and from the pit of material homogeneity, acquiring everything under the guidance of hyperphysical agencies, assisted by the accident of external conditions." Wolff's particular hyperphysical agency was a *vis corporis essentialis*—an essential organic force; but any phrase is as good as another in such matters The fact must be re-emphasized, that until the genetic continuity which links generation to generation was realized, until the origin of the germ-cells with their heritage of organization was elucidated, there could be no real progress in theories of development.

Von Baer.

Karl Ernst von Baer (1792–1876) brings us close to modern movements and modern methods. He handled the problems of development with a firmness of grasp which far surpassed that of his predecessors, and has not been excelled by his most illustrious successors. Von Kölliker has said of his works, that they may be unreservedly described as the most important contributions to embryological literature.

As a student of medicine at Dorpat he seems to have been influenced by Burdach, who was even then (1810–1814) lecturing on "the History of Life"; at Würzburg he sat at the feet of a remarkable teacher, Döllinger, who set his eager pupil to the practical study of comparative anatomy; but a perusal of Von Baer's charming autobiography convinces one that, even in early days, the student was much stronger than any of his masters. In spite of formidable difficulties he persistently worked his way towards the path of investigation which had from early days organically attracted him, and as the outcome of a long and arduous life he had the reward of leaving a stately scientific edifice, where there had been at the most only imperfect foundations.

As to Von Baer's work, though we cannot in our space do it justice, it may be noted, in the first place,

that while his predecessors had restricted their attention almost exclusively to the readily available chick, he has the credit of founding *comparative embryology*. As Bergh says, Von Baer broadened embryology as Cuvier had broadened anatomy, by making it comparative. He thus paved the way for Johannes Müller and his famous school, and there is a fairly continuous filiation from Von Baer to Balfour.

It was Von Baer, also, who first showed the importance of embryology as an aid to classification, and although his actual achievements in this connection are hardly acceptable nowadays, he has the credit of first suggestion. Even those who are now very cautious as to the use of "the embryological criterion of homology", will allow that without it the problems of relationship would be much more obscure than they are.

It was Von Baer who first clearly discriminated the great events in a life-history: (*a*) The primary processes of egg-cleavage, and the establishment of the germinal layers; (*b*) the gradual differentiation of the tissues (histogenesis); and (*c*) the blocking-out of the organs (organogenesis), and the shape-taking of the entire organism (morphogenesis).

But Von Baer is, perhaps, best remembered on account of his formulation of certain laws of development, which are discussed later on. What is often called "Von Baer's law", is the generalization that the individual development recapitulates the racial history, but it is by no means correct to father this hazardous conclusion on Von Baer. On the contrary, it was one of his endeavours to show that this generalization, carelessly credited to him, was far from correct.

The broadening out of embryological inquiry, which began with Von Baer, was continued in the work of Ratke, Kölliker, Lovén, Sars, Johannes Müller, Kowalevsky, Metschnikoff, and many others, until it became possible for Francis Balfour to gather up a thousand scattered papers into an ordered whole in his epoch-making work on comparative embryology (1880–1881).

Early in the century the poet Chamisso, who accompanied Kotzebue on his circumnavigation of the globe,

made a casual observation which has since become very famous. He observed that in a species of the free-swimming Tunicate, *Salpa*, a solitary form gave rise to embryos quite different in character and linked together in a chain, and that each link of the chain again produced a solitary form. His observation was not altogether accurate, but it called attention to a remarkable fact, which for a time seemed to stand alone.

Alternation of Generations.

The progress of marine zoology and the study of parasites, in the hands of men like Sars, Dalyell, Lovén, Von Siebold, and Leuckart, disclosed other alternations somewhat similar to that observed by Chamisso, but the results were not generalized until 1842, when Steenstrup (1813–1897) published a work entitled, *On the Alternation of Generations; or, The Propagation and Development of Animals through alternate generations, a peculiar form of fostering the young in the lower classes of animals.* From Hydroids (zoophytes) and Trematodes (flukes) he gave illustrations of the "natural phenomenon of an animal producing an offspring which at no time resembles its parent, but which itself brings forth a progeny that returns in its form and nature to the parent".

In 1838–39, as we have already noticed, Schwann and Schleiden formulated the cell-theory, towards which the researches of many workers had been steadily leading. In this doctrine there were three correlated conclusions: (*a*) that the organism has a cellular structure; (*b*) that its life depends on the reciprocal action of the component cells; and (*c*) that development means cell-formation, and begins by the cleavage of the ovum. "Every elementary part", Schwann said, "possesses a power of its own, an independent life, by means of which it would be enabled to develop independently, if the relations which it bore to external parts were but similar to those in which it stands in the organism. The ova of animals afford us examples of such independent cells, growing apart from the organism." Under the influence of the cell-theory it became the pressing task of the embryologists to

The Influence of the Cell-theory.

describe development in cellular terms. Some of the steps in this endeavour are of great historical moment, and must be discussed separately.

Nature of the Ovum.

Although Schwann and Schleiden clearly recognized that every multicellular organism, reproduced in the ordinary way, begins its individual life as a single cell, or, in other words that *the ovum is a cell*, this momentous conclusion required extension and corroboration. In 1828 Von Baer had discovered the mammalian ovum, and in 1861 Carl Gegenbaur demonstrated that the egg of every vertebrate animal is a single cell. Studies of invertebrates yielded the same result, and the discovery of the egg-cells of plants soon followed. Subsequent research has had nothing to add to this simple but fundamental fact; it has concerned itself with the organization of the egg and with the problem of its origin.

Nature of the Spermatozoon.

As far back as 1677 Louis de Hamen or Ludwig Hamm, a pupil of Leeuwenhoek, observed the spermatozoa of animals, and Hartsoeker claimed a priority of three years. This matters little, however, for neither understood what he saw. For long afterwards these essential male elements were regarded by many as parasitic animalcules wholly unrelated to development (hence the name "spermatozoa"), while other observers, nicknamed "spermatists" or "animalculists", believed them to be the earliest stages of the young animal, which found the nourishment necessary for development by entering the egg. Even Von Baer (1835) was inclined to interpret the spermatozoa as minute parasites peculiar to the male fluid; Johannes Müller seems also to have been in doubt; and Richard Owen included them in his article on "Entozoa" (internal parasites) in Todd's *Cyclopædia of Anatomy and Physiology*.

In 1786 Spallanzani showed that the sperms were essential to fertilization, since the filtered fluid was impotent; in 1837 R. Wagner emphasized their constant presence in all sexually-mature males; Von Siebold demonstrated their presence in the invertebrates; in 1841 Kölliker demonstrated their cellular origin in

the male organs or testes; in 1843 Martin Barry, an Edinburgh medical student, saw the union of sperm and ovum in the rabbit; in 1865 Schweigger-Seidel and La Valette St. George showed that the spermatozoon has a nucleus like other cells. Thus gradually was the simple fact demonstrated that *the spermatozoon is a cell.* Subsequent research has been concerned with studying the structure of the sperm, its mode of origin, and its behaviour in fertilization.

Fertilization.

In his forty-ninth exercitation, on "the efficient cause of the chicken", Harvey thus quaintly expresses what has always been, and still is, a baffling problem:—"Although it be a known thing subscribed by all, that the fœtus assumes its original and birth from the male and female, and consequently that the egge is produced by the cock and henne, and the chicken out of the egge, yet neither the schools of physicians nor Aristotle's discerning brain have disclosed the manner how the cock and its seed doth mint and coin the chicken out of the egge".

Baffling as the problem remains, it must be granted that great progress has been made in the later years of the Victorian era; many hundreds of researches directly bearing on fertilization have been published since 1875; the visible phenomena have been described in detail in a multitude of cases; and we have become much more definite as to what we wish to know.

On the old views as to the nature of fertilization we need not dwell; they were mere opinions without adequate basis of facts. Some said the ovum was all-important, and that the sperm merely supplied the awakening touch; others said that the sperm was all-important, and that the ovum merely supplied the necessary nutriment; and even when both elements were recognized as essential, vague ideas prevailed as to the nature of fertilization. De Graaf believed in an "aura seminalis" or seminal breath which passed from the male fluid to the ovum, and until 1854 Bischoff clung to the theory (which he then abandoned) that a mere touch of sperm and ovum was sufficient to ensure development.

The distinctively modern era in the history of fertilization dates from about 1875, when the brilliant researches of Auerbach, E. van Beneden, Bütschli, Fol, O. Hertwig, and others, showed that one of the essential phenomena in fertilization is the intimate and orderly association of the sperm-nucleus, of paternal origin, with the ovum-nucleus, of maternal origin, the result being the cleavage or segmentation-nucleus. The researches of Strasburger, De Bary, and others established the same result in regard to plants.

Subsequent research has been mainly concerned with deciphering the details of each step in the fertilization process, and with the attempt to ascribe a rôle or functional meaning to the different parts of the intricate cellular mechanism concerned in the act.

Maturation.

Although maturation precedes fertilization in time, its significance was longer in being appreciated. In 1824 C. G. Carus observed that little bodies (polar bodies, directive corpuscles, &c.) were given off by the ripe ovum of the water-snail *Limnæus*; Fr. Müller and Lovén made the same observation in 1848, and similar results gradually accumulated. In 1875 Bütschli showed that these little bodies were formed by the division of the ovum-nucleus, and Fol confirmed this a year afterwards. It was soon shown that in the majority of ripe ova it was a normal occurrence that the unfertilized nucleus should divide twice in rapid succession. In 1876 Giard interpreted the little bodies as abortive ova, a view which Mark also emphasized somewhat later (1881); and various other suggestions were made as to their meaning. In 1883, however, Van Beneden made the suggestive discovery that the sex-nuclei, which become intimately associated in the fertilization of the egg of the round-worm of the horse (*Ascaris megalocephala*), contain each one-half the number of nuclear elements or chromosomes characteristic of the *body-cells* of the species, and this has been confirmed in regard to numerous animals and plants. This led on to Weismann's theoretical interpretation, that the formation of polar bodies, and the analogous processes in the history of the spermatozoon, involved "reducing

divisions", whereby the germ-cells were prepared for their subsequent union in fertilization and the number of chromosomes was kept constant in the species. If it were not for the preparatory reduction the number of nuclear elements or chromosomes would be doubled at each fertilization. By the brilliant work of Platner, Boveri, O. Hertwig, and many others, for animals, of Guignard, Strasburger, and others, for plants, this fact at least seems to be securely established amidst a maze of uncertainties, that in the history of both male and female germ-cells the number of chromosomes is reduced to one-half of the number characteristic of the body-cells of the species.

Another embryological corollary of the cell-doctrine is that development implies cell-formation, or that the first step after fertilization is the cleavage or segmentation of the ovum.

The Mode of Development.

In 1826 Prévost and Dumas had given the first definite description of the cleavage of the frog's egg, showing that it first divides into two cells, then into four, then into eight, and so on; but the full import of the fact was not realized until later. Thus Schwann and Schleiden believed that cells might arise either by the division of a pre-existing mother-cell or by a process of "free cell-formation". In the latter case, as Wilson says, new cells were supposed to crystallize out, as it were, within a formative or nutritive substance, termed the "cytoblastema". "It required many years of research to show that 'free cell-formation' was a myth, though this had been suggested by many of Schwann's immediate followers, and though Virchow had, in 1855, positively maintained the universality of cell-division, contending that every cell is the offspring of a pre-existing parent cell. He summed up his position in the aphorism, *omnis cellula e cellula.*"

But Virchow's conclusion required detailed corroboration, and this was afforded by the early studies on ovum-segmentation and tissue-formation (histogenesis) associated with the names of Kölliker, Reichert, Remak, and many others.

Moreover, in combination with the facts beginning to

be established in regard to fertilization, Virchow's conclusion led on to two others of fundamental importance. The first of these was the conception of genetic continuity—that the ovum was derived by continuous cell-lineage from the fertilized ovum of the previous generation, and bears with it from the first an inherited organization. We shall return to this conception when we discuss Heredity; it is enough to notice here that it is the starting-point for every modern theory of development or inheritance, and removes the stumbling-block which was fatal to all the early theories. The apparently ready-made organization of the fertilized egg-cell, involving all the potentiality of the future organism, becomes less unintelligible when we recognize that it is, in a sense, itself an antiquity, a link in the continuous chain of germ-cells. We owe the first clear presentment of this idea to Virchow's classic work (1858).

The second corollary is one of great interest, practically as well as theoretically. Since the researches of O. Hertwig and others in 1875, it had been clear that each parent contributes a single germ-cell to the formation of the offspring; but the masterly researches of E. van Beneden (1883) showed that every nucleus of the offspring may contain nuclear substance derived from each of the parents, a conclusion which is visibly demonstrable for a few of the first steps in cleavage. In fact, Van Beneden to some extent *proved* what Huxley had foreseen when he said in 1878: "It is conceivable, and indeed probable, that every part of the adult contains molecules derived both from the male and from the female parent; and that, regarded as a mass of molecules, the entire organism may be compared to a web of which the warp is derived from the female and the woof from the male".

To Van Beneden and Boveri we also owe the discovery of the centrosomes—small bodies which seem to play an important part in the division of animal cells. They have been much discussed of recent years, and there is still great uncertainty in regard to them and their associated attractive spheres. One of the best-substantiated

conclusions is that of Boveri, who maintains that the ripe egg possesses all the organs and qualities necessary for division excepting the centrosomes, by which division is initiated. The spermatozoon, on the other hand, is provided with a centrosome, but lacks the substance in which this organ of division may exert its activity. Through the union of the two cells in fertilization all of the essential organs necessary for division are brought together; the egg now contains a centrosome which by its own division leads the way in the embryonic development. This is not the place to attempt a discussion of a very difficult problem, but we may cite the summing up given by one of the clearest of modern exponents—Prof. E. B. Wilson. "From the mother comes in the main the cytoplasm of the embryonic body, which is the principal substratum of growth and differentiation. From both parents comes the hereditary basis or chromatin by which these processes are controlled, and from which they receive the specific stamp of the race. From the father comes the centrosome to organize the machinery of mitotic division by which the egg splits up into the elements of the tissues, and by which each of these elements receives its quota of the common heritage of chromatin. Huxley hit the mark twoscore years ago when he compared the organism to a web of which the warp is derived from the female and woof from the male. What has since been gained is the knowledge that this web is to be sought in the chromatic substance of the nuclei, and that the centrosome is the weaver at the loom."

Germinal Layers.

The segmentation of the egg leads on to the establishment of the two primary germinal layers—the ectoderm or epiblast, and the endoderm or hypoblast. These layers are established in different ways in different types, but on the whole they give rise to similar structures throughout. The ectoderm forms especially the epidermis, the nervous system, and the foundations of the sense-organs, and a region at each end of the food-canal (fore-gut and mid-gut); the endoderm forms especially the lining of the mid-gut, and of the outgrowths which arise from it, and

also gives rise to the embryonic axis or notochord; while the rest of the body (such as muscles and skeleton) is mainly due to a third stratum of cells (mesoderm), which usually arises between the ectoderm and the endoderm.

For many years embryologists, from Von Baer onwards, were much concerned with the origin of these germinal layers, and with showing how they gave rise, separately or in combination, to the various organs of the body. It was held to be one of the criteria of complete homology, that anatomically similar organs should be traceable to an origin in similar layers. It was held that homology must be corroborated by "*homodermy*", and the fundamental similarity of the germ-layers throughout the Metazoa was the keystone of the so-called germ-layer theory (*Keimblättertheorie*); and it was in this connection a step of historical importance when Huxley (1849) collated the epiblast and hypoblast of the embryo with the two layers of cells which are seen in the structure of an adult polype, like the common hydra.

Gradually, however, the confidence of embryologists in this germ-layer theory has been shaken—by the following, among other considerations. (*a*) What one may call the stratification of the embryo is established in very different ways in different types; (*b*) there are some cases, notably sponges, where the products of the ectoderm and the endoderm cannot be readily brought into line with the state of affairs in the majority; (*c*) the mesoderm is so varied in its origin (from ectoderm, endoderm, or both), and in its occurrence, that the conception lacks even a pretence at unity; (*d*) in many cases the facts of development show that certain organs can be traced back to a few cells, specifically predestined from their first appearance, rather than to a homogeneous layer.

"It has become", E. B. Wilson says, "more and more clear that the germ-layer theory is, to a certain extent, inadequate and misleading, and that even the primary layers of the 'gastrula' cannot be regarded as strictly homologous throughout the animal kingdom.

To assume that they are so involves us in inextricable difficulties—such as those, for instance, encountered in the comparison of the Annelid gastrula with that of the Chordates, or the comparison of the sexual and asexual modes of development in Tunicates, Bryozoa, Worms, and Cœlenterates." . . . "The relationship of the inner and outer layers in the various forms of gastrulas must be investigated, not only by determining their relationship to the adult body, but also by tracing out the cell-lineage or cytogeny of the individual blastomeres from the beginning of development."

The Influence of Evolution-doctrine.

In stating what is called "the evidence for evolution" it is usual to refer to a series of embryological facts, such as the occurrence of gill-clefts in the embryos of higher Vertebrates, or the more or less fish-like stages in the development of the frog; but it is erroneous to suppose that the evolution-doctrine was, or can be, proved by the laborious induction of these and a thousand other facts. Embryological facts are only evidences of evolution in the sense that an acquaintance with them might possibly suggest the evolution-idea to an acute and unprejudiced mind, or in the sense that they are interesting and somewhat obtrusively puzzling phenomena, of which the evolution-theory furnishes a lucid interpretation, or in the sense that none of them contradicts the idea at the heart of the theory. There is no historical evidence which even suggests that the evolution-theory was arrived at by an inductive process, unless unconscious induction be included in the phrase. An adequate scientific doctrine should furnish an interpretation of the facts, which is self-consistent, and consistent with other doctrines, and this is what is claimed for the doctrine of descent. Therefore it must be said, that only a misunderstanding of the nature of scientific progress can explain the position of those who maintain that there is a vicious circle in corroborating the evolution-doctrine from embryology, and at the same time recognizing the evolution-doctrine as a suggestive influence in embryology.

As an instance of the influence of the evolution-

doctrine on embryology, we may refer to Hæckel's *Gastræa Theory* (1874). Here we have to distinguish between the observational basis and the inference drawn from it. The observational basis consisted in showing that one of the most frequent embryonic stages in animals is a two-layered sac,—the "gastrula"; it is very clearly seen in the development of sponge, star-fish, earth-worm, pond-snail, lancelet, and so on; in other cases its occurrence is disguised by the presence of a large quantity of yolk; in some other cases, *e.g.* mammals, it must be allowed that the gastrula is far to seek. At the same time it is certain that the gastrula is a very common embryonic stage, and Hæckel drew the inference that the ancestral form of multicellular animals was like a gastrula. He called this hypothetical ancestral type the Gastræa. For many years this theory was the centre of lively and fruitful discussion.

The Gastræa Theory.

The broadest generalization which has yet come from embryology is known as the Recapitulation Doctrine or biogenetic law, which expresses the conclusion that the individual development is in some measure a recapitulation of the racial history. The theory is an outcome of the *mutual influence* of evolution-theory and embryology.

The Recapitulation Doctrine.

In 1821 Meckel directed attention to the close similarity of the early embryonic stages in quite different animals, and spoke of "a correspondence between the development of the embryo and that of the entire animal series". The idea was also familiar to Oken, who gave it evolutionary significance, and did much to introduce it into biology.

Von Baer remarked on the close resemblances between the embryos of animals the adult forms of which are very different; a reptile-embryo, a bird-embryo, and a mammal-embryo are at certain stages very similar, and the illustrious embryologist confessed that he was unable to tell to which of these groups three unlabelled embryos before him really belonged. A careful examination of his "laws" shows, however, that he did not accept the recapitulation without many saving clauses.

He believed in it much less than many a modern embryologist, such as F. M. Balfour or A. Milnes Marshall. His "laws", as amended by Dr. John Beard, are as follows:—

"There is a stage in the development of every vertebrate embryo, during which, and only then, it resembles the embryo of any other vertebrate in a corresponding stage in certain general features. But, while it thus agrees exactly with any other embryo in this stage in characters which are common to all vertebrate animals, it differs from the embryo of any other class in certain special class-features, and also from any other embryo of the same class but of a different order, in other and ordinal characters. Immediately before this stage is reached, it begins to put on generic and specific characters, and thus it then begins to differ from all other embryos in these."

Louis Agassiz made one aspect of the recapitulation idea prominent in his teaching, and gave it clear expression in his famous "Essay on Classification" (1859). He rejected the evolutionist interpretation, but insisted on the correspondence between stages in embryonic development and the grades of differentiation expressed in the classification of living and extinct animals. "It may therefore", he said, "be considered as a general fact, very likely to be more fully illustrated as investigations cover a wider ground, that the phases of development of all living animals correspond to the order of succession of their extinct representatives in past geological times." His not less illustrious son, Alexander Agassiz, confirmed this in his detailed comparison between the fossil series of sea-urchins and the early stages in the development of modern forms. "Comparing the embryonic development with the palæontological one, we find a remarkable similarity."

In his *Facts for Darwin*, Fritz Müller expressed the recapitulation doctrine with great clearness, illustrating it from the life-history of Crustaceans. The larval stages which are often so striking, *e.g.* the common shore-crab, were interpreted as recapitulations of stages in the evolution of the race.

Hæckel has been one of the most convinced and luminous exponents of the idea of recapitulation, which he called "das biogenetisches Grundgesetz", and expressed in the now familiar words, "ontogeny tends to recapitulate phylogeny". He also drew the distinction between *palingenetic* characters, dating from the ancient ancestral stock, and *kainogenetic* characters, regarded as relatively recent adaptations.

Such is, at least, part of the intellectual pedigree of a theory which has had a profound influence on zoological embryology, and in much wider inquiries, throughout the Darwinian era. It seems to have found but little acceptance among botanists.

Of recent years there has been a strong reaction from belief in the recapitulation doctrine, and the reasons for this must be briefly considered.

(*a*) Everyone, of course, resents the popular travesties of the doctrine that have got afloat, *e.g.* that the human embryo is at one stage like a little fish, later like a little reptile, and so on; but it will be admitted that even the doctrine of evolution suffers similar violence. (*b*) Although even an expert embryologist, such as Milnes Marshall, may have said, "Every animal in its own development repeats its history, climbs up its own genealogical tree", we know that this was meant "in a wide and metaphorical sense". As Hæckel has clearly emphasized, the recapitulation asserted is general, not exact, there is frequently a tendency to abbreviation, and kainogenetic adaptations may disguise the palingenetic features. It hardly needs to be mentioned that one term in the comparison, the phylogeny, is in most cases very imperfectly known either from the actual fossil records or from the inferences of the comparative anatomists. (*c*) The recapitulation-theory was not intended as a contribution to the physiology of development, but rather as an historical interpretation. It is, so to speak, a light from a distance, and does not touch the question of the immediate conditions which lead on from stage to stage. It is a fact that the frog ovum gives origin to a larva with various fish-like structures —gill-slits, gills, two-chambered heart, &c.; it is a

truism that these develop because of immediately operative growth-conditions, or reactions between inherited organization and environmental stimulus; but the whole story becomes more luminous to us if we are otherwise assured that the race of frogs sprang from a fish ancestry. (*d*) It is said that increased precision of embryological work discloses individual characteristics at a very early stage in ontogeny, that even a blind man could distinguish embryos of duck from those of the fowl as early as the second or third day of incubation. Yet this does not seem to be inconsistent with a general recapitulation.

All are agreed that there is no completeness of recapitulation, else phylogeny would be a simpler business than it is. As Hæckel, Balfour, and others have said, ancestral stages may be dropped out in embryonic development, or disguised by newer adaptive characters in larval development. But in the dropping out there must be some law. Why do certain ancestral characters recur, or apparently recur, while of others there is no trace? Why does an embryo snake show gill-clefts but no trace of fore-limbs? To this question Balfour answered, "It is very possible that rudiments of the branchial arches and clefts have been preserved because these structures were functional in the larva (Amphibia) after they ceased to have any importance in the adult; and that the limbs have disappeared even in the embryo, because in the course of their gradual atrophy there was no advantage to the organism in their being preserved at any period of life".

Similarly, Prof. Sedgwick has maintained that when there is a recapitulation of ancestral stages in *embryonic* development, this implies that the characters in question were retained as useful *larval* characters for a long time after they had ceased to be directly functional in the adult.

Substitution of Organs.

Another evolutionary idea which has arisen out of embryology is that of "the substitution of organs", suggested by Nicolaus Kleinenberg (1842–1897), one of Hæckel's numerous disciples, and professor of zoology at Messina and Palermo. He

published only a few (eleven) papers, but some of these were of great value, especially his account of the development of *Hydra* (1872), of *Lumbricus trapezoides* (1878), and of the Polychæte worm *Lopadorhynchus* (1886). In his memoir on *Lopadorhynchus* he dealt very severely with the conception of the mesoderm as an independent germinal layer, and sketched his theory of the substitution of organs. This may be explained by taking a concrete instance.

In all Vertebrate embryos there is, for some time at least, a supporting axial rod or notochord, developed along the dorsal median line of the primitive gut. This persists throughout life in the lancelet and lamprey and a few old-fashioned types, but from Fishes onwards it is gradually replaced in development by the backbone. The notochord does not become the backbone, which has a different (so-called mesodermic) origin, but is replaced by it. The notochord is a temporary structure, around which the vertebral column is constructed, as a tall brick chimney might be built around an internal scaffolding of wood. Now, what is the relation between the more primitive axis or notochord and its more effective substitute the backbone, seeing that the former does not become the latter? Kleinenberg's suggestion was that the notochord supplies the stimulus, the necessary developmental condition, for the formation of the backbone when suitable materials are forthcoming. Of course we require to know more about the way in which the old-fashioned structure prepares the way for and stimulates the growth of its future substitute, but the general idea of one organ leading on to another is suggestive. It is consistent with our general conception of development—that each stage supplies the necessary condition for the next; it helps us to understand more clearly how new structures, too incipient to be functional, and old structures, too transitory to be of direct use, may persist; in short, it makes the process both of development and evolution more intelligible.

Kleinenberg maintained that the Annelids possessed two quite distinct nervous systems, one for the larva, and the other for the adult, which are not homologous

any more than notochord and backbone are; and he extended this to the nervous system of vertebrates—a difficult path which Dr. Beard has followed.

Experimental Embryology.

The newest departure in embryological investigation has been along experimental lines, and there is no better illustration of modern biological activity. Within a few years a vast literature has accumulated, an important journal—Roux's *Archiv für Entwicklungsmechanik*—has arisen as a specialized record of research, and there is already a text-book (Haacke's) on the subject. The investigations are still too novel and incomplete to be securely appreciated, but there can be no doubt that they have shed fresh light on old problems, and that they are full of promise. It seems fair to associate one name in particular with this new movement—that of Wilhelm Roux, the keen-witted author of *Der Kampf der Theile im Organismus* (1881)—The struggle of parts within the organism,—but his work has been ably criticised, or supplemented, or extended, as the case may be, by Oscar Hertwig, Born, Chabry, Driesch, Herbst, Morgan, Wilson, and others. The experimental work is especially of two kinds: (1) subjecting developing ova to new conditions of chemical medium, pressure, gravity, temperature, &c.; (2) puncturing or isolating certain cells of the segmenting ovum and observing results. The results have immediate relation to several problems: (*a*) the morphological problem of cell-lineage, (*b*) the physiological problem of immediate growth-conditions or body-physics, (*c*) the theory of development, and (*d*) the influence of the environment in inducing modifications.

Theories of Development.

There are at present two main theories of development—the mosaic theory of Roux and Weismann, and the anti-mosaic theory of Hertwig and Driesch. In their extreme forms these two theories are irreconcilable, but with mutual concessions it seems possible to combine them.

According to the mosaic theory, the cause of differentiation is to be found in the nature of cell-division, which is supposed to be *qualitative*, sifting out different characteristics into the two daughter-cells. Thus if the

original cell had the qualities *abcxyz*, it is supposed that its two daughter-cells might have the qualities *abcxy* and *abcxz*. And what each cell becomes, is from the first determined by the particular contingent of vital qualities with which it starts.

According to the anti-mosaic theory, cell-division is *quantitative*, *i.e.* without any sifting out of vital units, and the cause of differentiation is to be found in the varied relations in which the cells find themselves. The prospective value of embryonic cells, Driesch says, is "a function of their location". Each of the early cells is supposed to have a complete set of specific characteristics, but some remain latent while others become active, this being determined by the relations of the particular cell to the whole of which it forms a part.

These two theories, over which a long-drawn-out battle has been fought, agree in recognizing a complex organization in the ovum. Although we cannot see it, or even imagine it, there must be in the egg a complex architectural arrangement of some sort, corresponding to the hereditary qualities. The two theories differ as to the manner in which differentiation occurs, the first relying on the hypothesis of qualitative division, the second on the hypothesis of cellular interaction.

The two most serious objections to the mosaic theory are: (1) that there is no proof forthcoming of qualitative cell-division; and (2) that an isolated cell from the 2-cell or 4-cell stage of a developing ovum may, in many cases (lancelet, sea-urchin, &c.), give rise to an entire embryo.

The most serious objections to the anti-mosaic theory are found in those cases where even the first cleavage of the egg results in two unequal cells, as in *Nereis*, the reason for this being some unknown predetermination within the ovum.

Chapter XI.

Heredity.

A Modern Study—The Facts of Inheritance—Problems of Heredity—Theories as to the Uniqueness of the Germ-cells—The Doctrine of Germinal Continuity—Elaborations of the Idea of Continuity—The Problem of Reconstruction—Inheritance of Acquired Characters—Criticisms of Weismann's Position—Filial Regression—Galton's Law of Ancestral Inheritance.

A Modern Study.

It must be admitted, even by the most pessimistic, that the biologists of the Victorian era have made some progress in the understanding of heredity, or the relation between successive generations. But if we measure what we can honestly say we *know* in regard to heredity by what we should like to know, we must confess that the serious study of the subject has just begun.

The great steps in the Darwinian era have been: (*a*) the exposition of the doctrine of germinal continuity, (*b*) a more precise investigation of the material basis of inheritance, (*c*) the growth of scepticism as to the inheritance of acquired characters, and (*d*) the application of statistical methods which have led to the formulation of the law of ancestral heredity and the like. The most important names are those of Weismann and Galton, and the most fruitful methods have been (1) detailed microscopic analysis as to the cellular phenomena of reproduction, and (2) statistical researches as to the facts of inheritance. What seems most needed at present is a series of exact experimental studies in breeding, continued through a series of generations.

The facts of Inheritance.

The general facts of Inheritance were first adequately discussed in a classic work by Lucas (1847–1850). At present they may be summarized as follows: (1) The general likeness between parent and offspring is a commonplace of observation, condensed in the familiar saying, "Like begets like". As variations which make the offspring different from the parent

continually occur, in other words, as resemblance is often *incomplete*, the formula has to be altered to "Like *tends* to beget like". (2) Besides the general resemblance, which expresses the relative constancy of the species, a particular similarity is often demonstrable. The offspring reproduces not only the general features, but often minute characteristics of its parents, or of one of them, and this applies to abnormal as well as to normal characters. (3) In many instances the offspring exhibits, not only parental, but also grandparental characteristics; the inheritance of an organism may be compared to a mosaic built up from many ancestors. As Galton has shown, each parent contributes on an average to the heritage of the offspring one-fourth, each grandparent one-sixteenth, and so on. (4) The fact in regard to the explanation of which most debate at present obtains, is that characters individually acquired by the parent as the results of environmental or of functional influence, may *reappear* in the offspring. (5) Throughout successive generations there is, Galton maintains, a tendency to sustain the specific type or average, by the continued approximation of the progeny of exceptional forms towards the mean of the species.

Problems of Heredity.

There are at present three main problems of heredity, which must be carefully distinguished, as has not always been done.

1. What accounts for the unique character of the germ-cells?
2. Granted the unique character of the germ, what are the conditions of its reconstructing a form like the parent?
3. What are the facts in regard to the reappearance of individual peculiarities or modifications, acquired by the parent as the result of changes in function or environment? Are they transmissible?

(*a*) *Early Hypotheses.*—We need not, however, discuss the possession of the germs by spirits, nor yet the postulates of *vires formativæ*, *nisus formativus*, principle of heredity, *Vererbungskraft*, or *Bildungstrieb*, but begin

with the gradual emergence of the theories of heredity into fuller scientific daylight. It is only necessary to linger for a little over the preformationist hypotheses to which we have already referred (chap. x.). According to the extreme preformationists, such as Haller, the egg or the male element was supposed to contain an excessively minute micro-organism, a complete though miniature model of the adult. This was supposed to be stimulated from potential to actual life by fertilization. By the absorption of nutriment in its interstices it was supposed to unfold, expand, or "evolve" into the adult organism. The "animalculists" found this miniature model in the male element, which was believed to be nourished by the ovum, while the "ovists" held that the model lay *in nuce* within the egg, and was, so to speak, awakened by the sperm. This hypothesis was further backed up by that of "*emboîtement*", according to which the germ was not only itself a marvellous micro-organism, but contained in ever smaller proportions, after the manner of an infinite juggler's-box, the miniature models of the generations to follow. But how the germ became endowed with its marvellous supposed organization was left an unsolved riddle.

Theories as to the Uniqueness of the Germ-cells.

It must be allowed that, in their general proposition that the germ was a potential organism, the preformationists were correct. The germ cell *does* imply the future organism, and future generations of organisms as well. But the preformationists exaggerated this idea into a denial of individual development, and in default of any theory as to the origin of the initial organization of the germ-cell they were forced to fall back on mystical or metaphysical verbalism. The early researches of Wolff alone were quite sufficient to show that neither the extreme theory of preformation nor its consequent hypothesis of *emboîtement* had any basis of fact. For Wolff showed that there is no preformed model, but that there is a visible development of the apparently simple into the obviously complex. Yet as he also was unable to throw any light upon the inevitable question, "How does this apparently simple germ-cell come to have such

unique potentialities?" he too was forced to fall back upon mysticism.

(*b*) *Special Pangenetic Theories.*—Passing from the early hypotheses, we come to a series of theories, which are in varying degrees scientific, and may be fairly enough described by the general designation *pangenetic.* They have this in common, that they seek to explain the uniqueness of the germ-cell by regarding it as a centre of contributions from different parts of the organism.

At such different epochs as are suggested by the names of Democritus and Hippocrates, Paracelsus and Maupertuis, incipient theories of pangenesis—prophecies of Darwin's—were suggested. Thus Democritus maintained that the "seed" of animals was elaborated by contributions from all parts of the body. Two thousand years later, Buffon again regarded the germs as mingled extracts from all parts of the body, or as collections of samples from the various organs. If such were indeed the case, Buffon and his predecessors saw no further difficulty, for each contributed sample was supposed to reproduce in the embryo a structure like that from which it originated in the parent.

In 1864, in his *Principles of Biology*, Herbert Spencer suggested the existence of "physiological units", derived from and capable of development into cells, and supposed that they accumulated in the reproductive elements, which thus became, in some conceivable sense, miniature organisms.

The best-known theory of this class is, of course, the "provisional hypothesis of pangenesis" suggested by Darwin in his *Variation of Animals and Plants under Domestication*:—

(1) Every cell of the body, not too highly differentiated, throws off characteristic gemmules;

(2) These multiply by fission, retaining their characteristics;

(3) They become specially concentrated in the reproductive elements;

(4) In development the gemmules unite with others like themselves, and grow into cells like those from which they were originally given off.

The applications of this, in one sense, very satisfactory theory to the phenomena of atavism, and reappearance of similar characters at similar times, do not concern us in this general survey. Its great defect, obvious, of course, to its author, was its entirely hypothetical character. No one has ever observed any gemmules; their migration, collection, and development are equally hypothetical.

Another theory, that of Jaeger, is somewhat difficult to summarize, partly because of its technical character, partly because the author does not appear to have been quite consistent. The main points, under the present section, are the following:—

(1) Each organ and tissue contains, along with the molecules of its albumen, a specific "scent-and-flavour-stuff".

(2) In hunger and similar experience the albumen liberates the "stuffs", which then penetrate through the body as fatty acids, ethers, &c.

(3) These are particularly attracted to the reproductive cells, and may be said to specialize the germinal protoplasm.

From experiments on the transfusion of blood, Galton was led to conclude that "the doctrine of pangenesis, pure and simple, is incorrect". But he did more than urge serious objections against Darwin's theory; he formulated one of his own, to which subsequent investigators have rarely done sufficient justice. The more important part of Galton's theory will be discussed in its proper place; it is not included in the series of pangenetic hypotheses. Galton is, in fact, one of the numerous biologists who have *suggested* the continuity of the germinal protoplasm. He is included at this stage, however, because he admitted as a subsidiary hypothesis a limited amount of pangenesis. To account for those cases which suggest that characters acquired by the individual parent are "faintly heritable", Galton supposed that "each cell may throw off a few germs that find their way into the circulation, and have thereby a chance of occasionally finding their way to the sexual elements, and of becoming naturalized among them".

In 1883, in his valuable work entitled *The Law of Heredity*, Professor W. K. Brooks gave full expression to a modification of Darwin's view of pangenesis. The main positions, which are here relevant, may be summarized as follows, almost in the author's words:—

(1) The male and female cells are specialized in different directions; their union gives variability.

(2) The ovum is a cell which has gradually acquired a complicated organization, and which contains material particles of some kind to correspond to each of the hereditary characteristics of the species.

(3) The ovum reproducing its like, as other cells do, gives rise not only to the divergent cells which build up the body of the organism, but also to cells like itself, which are the future reproductive cells.

(4) Each cell of the body has the power to throw off minute germs. The cell does this especially when some change in its environment has disturbed its functions.

(5) These germs may be carried to all parts of the body. They may penetrate to an ovarian ovum or to a bud, but the male cell has gradually acquired, as its especial and distinctive function, a peculiar power to gather and store up germs.

(6) In fertilization each germ or gemmule unites with that particle of the ovum which is destined to give rise in the offspring to the cell which corresponds to the one which produced the gemmule, or else it unites with a closely-related particle, destined to give rise to a closely-related cell. Such a cell will be a hybrid, tending to vary.

(7) As the ovarian ova of the offspring share by direct inheritance all the properties of the fertilized ovum, the organisms to which they give rise will tend to vary in the same way.

(8) A cell which has thus varied will continue to throw off gemmules, and thus to transmit variability to the corresponding part in the bodies of successive generations of descendants, until a favourable variation is seized upon by natural selection.

(9) As the ovum which produced this selected organism will transmit the same variation to its ovarian ova by direct inheritance, the characteristic will be established as specific, and transmitted henceforth without gemmules.

The above theory, being important, has been stated at some length. Apart from the suggestion of variation as due to sexual intermingling, with which Weismann has made us more familiar; apart, too, from the suggestion of germinal continuity, the credit of which

Brooks shares, there are several subsidiary hypotheses in the modification which he has proposed. It is in *unwonted and abnormal* conditions that the cells of the body throw off gemmules; the *male* elements are the special centres of their accumulation; it is the ovum that keeps up the *general* resemblance between offspring and parent.

The theory of "Pangenes" advocated by De Vries in 1889 is hardly in any sense a rehabilitation of Darwin's, since it rejects the hypothesis of "transport", and incorporates the distinctively modern conception of germinal continuity. It has often been urged that the hypothesis of pangenesis involves not one but many suppositions—that it is just as difficult to understand why a gemmule should reproduce a cell like its own origin as to understand the entire problem, and so on. Detailed criticism will be found in the works of Galton, Ribot, Brooks, Herdman, Plarre, and others. It is enough to emphasize the comparative gratuitousness of any special theory whatever, a paradox which is explained in the succeeding section.

The Doctrine of Germinal Continuity.

As far back as 1849 Owen pointed out in his paper on Parthenogenesis that in the developing germ it was possible to distinguish between cells which became much changed to form the body, and cells which remained little changed and formed the reproductive organs. This was probably the earliest distinct suggestion of the modern theory of germinal continuity, but Owen seems to have virtually abandoned it later on.

In 1866, in his classic *Generelle Morphologie*, Haeckel emphasized the simple and yet fundamental fact of the material continuity of offspring and parent. In a historical note upon the distinction between the "personal" and "germinal" parts of an organism, Rauber states that the distinction was proposed by Haeckel in 1874, and by himself in 1879.

Jaeger stated the doctrine of germinal continuity very clearly and concisely at an early date (1878):—"Through a great series of generations the germinal protoplasm retains its specific properties, dividing in

every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as *the continuity of the germ protoplasm*." . . . "Encapsuled in the ontogenetic material, the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters."

Brooks notes that, in papers published in 1876 and 1877, he had also suggested the notion of germinal continuity, and the conception is clearly expressed in his work already quoted: "The ovum gives rise to the divergent cells of the organism, but also to cells like itself. The ovarian ova of the offspring are these latter cells, or their direct unmodified descendants. The ovarian ova of the offspring share by direct inheritance all the properties of the fertilized ovum."

The important theory of Galton now requires notice. Two preliminary notes are requisite. Galton was extremely doubtful in regard to the genuine *transmission* of acquired characters. It was to account for the possible faint inheritance of some of these that he admitted, as a subsidiary hypothesis, a limited amount of pangenesis. In the second place, it is needful to notice Galton's term "stirp", which he used to express the sum total of the germs, gemmules, or organic units of some kind, which are to be found in the newly-fertilized ovum.

(1) Only some of the germs within the stirp attain development in the cells of the "body". It is the dominant germs which so develop.

(2) The residual germs and their progeny form the sexual elements or buds. The part of the stirp developed into the "body" is almost sterile. The continuity is kept up by the undeveloped residual portion.

(3) The direct descent is not between body and body, but between stirp and stirp. "The stirp of the child may be considered to have descended directly from a part of the stirps of each of its parents; but then the personal structure of the child is no more than an im-

perfect representation of his own stirp, and the personal structure of each of the parents is no more than an imperfect representation of each of their own stirps."

This is a definite expression of the notion that the germinal cells of the offspring are in direct continuity with those of the parents. The antithesis between the "soma" and the chain of sex-cells is emphasized.

The history must also include Nussbaum, who called emphatic attention to the very early differentiation and isolation of the sex-elements to be observed in some cases. The theory both of Jaeger and of Nussbaum is that of a continuity of germinal *cells*. The theory of Weismann is more strictly that of the continuity of germinal *protoplasm*.

The idea of a continuity of germ-*cells* may now be summarized more definitely:—

(1) At an early stage in the embryo, the future reproductive cells of the organism are often distinguishable from those which are forming the body.

(2) The latter develop in manifold variety, and lose almost all likeness to the mother germ.

(3) The former—the reproductive rudiments—are not implicated in the differentiation of the "body", remain virtually unchanged, and continue the protoplasmic tradition unaltered.

(4) As the sex-cells of the offspring are thus continuous with the parental sex-cells which give rise to it, they will in turn develop into similar organisms.

This fact of the continuity of reproductive elements is obviously of fundamental importance. If a fertilized egg-cell has certain characters, *a*, *b*, *c*, *x*, *y*, *z*, it develops into an organism in which these characters, *a*, *b*, *c*, *x*, *y*, *z*, are expressed; but, at the same time, the future reproductive cells are early set apart, retaining the characters *a*, *b*, *c*, *x*, *y*, *z*, in all their entirety, to start a new organism again with the same capital. Balbiani, who was not influenced by theoretical considerations, observed in the development of the blood-worm or *Chironomus* (an insect) that the future reproductive cells were isolated before even the blastoderm was completed; that is to say, at a stage when hardly any differentiation had

occurred, a portion of the unchanged ovum was insulated to continue the constancy of the species.

In this aspect the reproductive cells form a continuous chain, and the reproduction of like by like is as natural and necessary as it is in the Protozoa. No special theory is required. Similar material in similar conditions produces similar results. But a serious difficulty besets this doctrine. Such an early appearance and insulation of the reproductive cells, continuous with the very ovum itself, does indeed occur, and where it does this part of the problem of heredity is simple. Early origin of special germ-cells, distinguished from those of the general "body", has been observed in leeches, *Sagitta*, thread-worms, many Polyzoa, *Moina* among crustaceans, not a few insects, Phalangidæ among spiders, and the Teleostean fish *Micrometrus aggregatus*, while indications of the same early separation are not wanting in a number of other organisms. But it must be distinctly allowed that in most cases it is only after differentiation is relatively advanced that the future reproductive cells make their appearance. Thus we have to pass from the cases of the continuity of the germinal *cells*, to the more general, but less objective fact of the "continuity of the germ-*plasm*".

Weismann's Theory.—Weismann, like the previous investigators, reached his conclusion independently. In the fact of continuity between the reproductive elements of generations, the solution of likeness must be found. But a direct chain of cellular continuity has been demonstrated only in a few cases. The solution which is proposed for the majority of cases is as follows:—

(1) "In each development a portion of the specific germ-plasm (*Keimplasma*), which the parental ovum contains, is not used up in the formation of the offspring, but is reserved unchanged for the formation of the germinal cells of the following generation."

(2) What is actually continuous is the germ-plasm "of definite chemical and special molecular constitution". A continuity of germinal cells seems to be relatively rare; a continuity of intact germ-plasms is constant.

(3) This germ-plasm has its seat in the nucleus, is extremely

complex in structure, but has nevertheless great powers of persistence and of growth.

Elaborations of the Idea of Continuity.

It may now be concluded that in the more or less strict continuity of the successive sets of reproductive elements lies the solution of the main problem of heredity. This appears the most convenient place to notice various suggestions made as to what it is exactly that is continuous. The earlier of these suggestions were brought forward indeed before the notion of continuity had its present definite form, but it seems appropriate to introduce them here.

The Memory Theories.—Prof. Hering in Prag and Mr. Samuel Butler in England suggested about the same time a psychical aspect of the hereditary continuity. The two suggestions may be so far summed up together. Memory is a general function of organized matter, and the reproduction of parental likeness is the result of unconscious recollection of the past. What are ordinarily called memory, habit, instinct, and embryonic reconstruction are all referable to the memory of living matter. Hering finds the basis of this unconscious memory in the persistence of the undulatory movements supposed to be characteristic of the molecules. These undulations are sensitive to change, and room is thus left for variability, but their tendency to persist in their established harmony is the basis of heredity.

Hæckel also emphasized the luminous metaphor of "organic memory", and sought to express it in terms of molecular motion. His theory is summed up in the characteristic phrase "perigenesis of the plastidules". Comparing the course of phylogenetic development to a complex, ramified series of wave-lines, in which a single life is represented by a single wave, he imagines a similar ontogenetic wave-motion in the development of the individual. "The developing impulse which in the one case is transferred from the ancestral species to the whole group of species, and in the other case from the ancestral cell to the entire group of cells, assumes in both cases the same form of a branching wave-motion."

"The true and ultimate *causa efficiens* of the biogenetic process, I propose to designate by a single word, Perigenesis—the periodic wave-generation of the organic molecules or plastidules." The tendency that this periodic motion has to persist, preserving as it were a characteristic rhythm, explains the relative constancy of ordinary inheritance, while at the same time the results of new experience may be added on to the dominant molecular movement. In very simple organisms, as he says, the plastidules have, so to speak, learned little and forgotten nothing, while in highly-perfected types the plastidules have both learned and forgotten much.

According to Jaeger the continuity is protoplasmic, and is effected after the ordinary fashion of cell-division. To this there has to be added his chemical conception of pangenesis, which, when expressed in more modern phraseology, is the supposition that characteristic chemical substances find their way to the reproductive elements, and make these, to some limited extent, sharers in the general life of the organism.

Galton does not make the continuity much more precise than is implied in the general statement that a residue of the germs, gemmules, or organic units in the "stirp", remaining latent in the construction of the body, are passed on into the reproductive elements, and keep up a continuity between "stirp" and "stirp". In regard to the future history of the gemmules, Galton supposes that they form groups in the ovum, and become directly associated with its division, while at later stages they wander and give rise to new cells. To obviate histological difficulties, Herdman proposes the following reasonable amendment, "that the body of the new individual is formed, not by the development of gemmules alone and independently into cells, but by the gemmules in the cells causing, by their affinities and repulsions, these cells so to divide and redivide as to give rise to new cells, tissues, and organs". Brooks and Nussbaum rest satisfied in maintaining a cellular continuity.

What keeps up the continuity, according to Weis-

mann, is the germ-plasm, *i.e.* a special portion of the nuclei of the reproductive cells, which, with great morphological stability, keeps itself intact, and is sooner or later re-established in the reproductive cells of the growing organism. Nägeli finds sufficient explanation of the constancy of inheritance in the individuality and persistence of what he calls the "idioplasm".

Kölliker, O. Hertwig, Strasburger, and Bambeke may be noted for the emphasis which they have laid upon the nuclei as transmitting or rather continuing the essential characteristics from generation to generation. Thanks to the researches of such investigators as Van Beneden and Boveri, it is now certain that the male and female nuclei contribute an equal share in forming the segmentation-nucleus of the ovum. Nay more, each of the first two daughter-cells has in its nucleus half of the male and half of the female nuclear elements, and it is possible that this marvellously exact dualism holds true later on.

Most daringly, perhaps, has the continuity been expressed by several, *e.g.* Berthold, Gautier, and Geddes, in chemical terms. In a paper by the last-mentioned on "Growth, Sex, Reproduction, and Heredity", the following weighty sentence occurs:—"If the reproductive elements start with a specific protoplasm continuous with that of the combined mother ovum and fertilizing sperm—that is, with a concentrated accumulation of characteristic anastates and katastates—the simple fact that the products of protoplasmic change must be fixed, definite, and continuous, as in all chemical processes, gives us at once a protoplasmic basis from which to explain the constant and necessary symmetry of segmentation and development". The views of Berthold are closely similar. Inheritance is possible only on the basis of the fundamental fact that in the chemical processes of the organism "the same substances and mixtures of substances are reproduced in quantity and quality with regular periodicity". Gautier discusses both variation and heredity from a chemical point of view. "The force which maintains the species, and gives it the character of constancy and resistance,

is nothing more than the resultant of the forces which maintain the *chemical species* of which the organism is composed."

What may be called the dominant modern view is summed up in the word *organization*. What the germ-cell inherits from the parental germ-cells is an organization of great complexity. Of the nature of this organization we know nothing, but it is possible to think of it as an intricate architecture of minute particles which are the material bearers of particular qualities. To these hypothetical units numerous names have been given—biophors, pangenes, idiosomes, &c. &c.

The Problem of Reconstruction.

The doctrine of the continuity of the reproductive protoplasm not only answers the first question as to the uniqueness of the germ-cell, but thereby casts a new light upon the problem of reconstruction. The problem is simplified, and, to a certain extent, disappears. Why should the germ-cell divide, redivide, and build up an embryo in the precise way in which it does? Because it is virtually continuous with the parent germ, which behaved in a precisely similar fashion. Thus the question ceases to be particular, and becomes general—ceases, in fact, to be a problem in heredity, and becomes a subject for investigation under the mechanics of development.

This, it need hardly be said, is to refer to a field of investigation which has been but little worked. In spite of the luminous suggestions of His, Rauber, Roux, and others, there are few general facts on which one can find foothold for further construction. Yet the task has been more than begun in the investigations of the enthusiastic modern school of experimental embryologists. Such current phrases as "cellular dynamics", "protoplasmic mechanics", "developmental mechanics", "physiological morphology", indicate the trend of modern research.

"To think that heredity will build organic beings without mechanical means is a piece of unscientific mysticism", as Professor His has said, and yet the tendency does not rapidly disappear from even scientific literature. To say that "ontogeny recapitulates phylogeny", or

that "the microcosm of the ontogenetic tree is a reflection of the macrocosm of the genealogical tree", is to express a marvellous generalization, to the dangers of which we have already referred. What we wish to understand is, as Hallez expresses it, how the protoplasm is, at each stage, the architect as well as the material of its own development. The metaphors of memory and recapitulation suggest that the developing organism has somehow a feeling for history, or that the dead hand of the past is literally upon the present, while our aim must be to get beyond mere phrases, and to understand the chemical and physical conditions which, more or less modified in the course of history, must still be present to rule each step in the development.

There can be no doubt that, in the modern theory of continuity, there is found the reconciliation between those who maintain that the likeness of offspring to parent is due to the presence of similar conditions, and those who are satisfied in referring the resemblance simply to "heredity". That there is similar material to start with is one half of the truth; that there are similar conditions throughout the development is the other.

Inheritance of Acquired Characters.

The third problem, which we stated at the outset, concerns the inheritance of acquired characters. It is well known that many organisms in the course of their individual life are affected by environmental influences, or by use and disuse of their organs. Thus there result what are conveniently called "modifications"—environmental and functional changes in the body of the individual organism. The question is, whether these may be transmitted to the offspring by the parent which acquires them. Two cautions may be noted in starting: (1) No naturalist doubts the inheritance of *constitutional or organismal* variations. These may be reasonably traced back to the fertilized egg-cell. But what is involved in the fertilized egg-cell may also be by hypothesis involved in the germ-cells which give rise to the next generation. There is no argument on this fact; the present scepticism relates to functional and environmental

modifications. (2) No one doubts that functional and environmental variations often *reappear*. Many doubt, however, that they reappear *because* they have been transmitted. Another alternative is obviously open. The conditions which originally brought about a given change may still persist, and may hammer the same effect upon the offspring which they wrought upon the parent.

Doubt as to the transmission of acquired characters is certainly not novel, though Weismann has the credit of crystallizing out the scepticism. Brock has noticed that the editor, whoever he was, of Aristotle's *Historia Animalium* seems to have differed from his master on this subject. Aristotle had referred to the inheritance of the exact shape of a cautery mark; but the editor insinuated a doubt as to apparent instances of this sort.

In modern times Kant was one of the first to express a firm disbelief in the transmission of individual peculiarities, and Bonnet was of the same opinion, but neither seems to have defined exactly what they intended to exclude from inheritance.

James Cowles Prichard (b. 1786), a well-known anthropologist, anticipated as early as 1826 some of the characteristically modern views on evolution. His importance has been recently expounded by Prof. E. B. Poulton. In the second edition of his *Researches into the Physical History of Mankind* (1826) Prichard stated the case in favour of organic evolution, recognized the operation of natural and artificial selection, and not only drew a clear distinction between acquired and congenital characters, but argued that the former were not transmitted. He was not rigidly consistent, and his convictions seem to have weakened in after years, but his anticipation of one of Weismann's positions by more than half a century is remarkable.

Galton preceded Weismann not only in abandoning the Lamarckian position, but also in outlining the conception of germinal continuity. Galton had been led to doubt the transmission of acquired modifications, partly on general grounds and partly because his experiments on the transfusion of blood in rabbits had forced him

to give up all belief in Darwin's theory of pangenesis. After an examination of the evidence in support of the Lamarckian postulate Galton summed up as follows:—

"The inheritance of characters acquired during the lifetime of the parents 'includes much questionable evidence, usually difficult of verification. We might almost reserve our belief that the structural cells can react on the sexual elements at all, and we may be confident that at the most they do so in a very faint degree —in other words, that acquired modifications are barely, if at all, *inherited* in the correct sense of that word.'

(1) In regard to climatic variations, Galton doubts any reaction of the 'body' upon the germs, but believes that the germs are themselves directly affected.

(2) The same is true in many constitutional diseases that have been acquired by long-continued irregular habits.

(3) The cases of the apparent inheritance of mutilations are outnumbered by the overpowering negative evidence of their non-inheritance.

(4) The case of Brown-Séquard's hereditarily epileptic guinea-pigs, in consequence of an operation performed upon the parents, is *perhaps* interpretable as the result of imitative influence.

(5) It is hard to find evidence of the power of the personal structure to react upon sexual elements, that is not open to serious objection. That which appears the most trustworthy lies almost wholly in the direction of nerve changes, as shown by the inherited habits of tameness, pointing in dogs, and the results of Dr. Brown-Séquard."

Weismann, however, has the credit of having brought the scepticism to a climax. He denied all inheritance of acquired characters, finding no convincing evidence that characters impressed upon the parental organism by the surroundings, or acquired as the result of use and disuse, can be transmitted. More than that, however, Weismann's whole theory of variation, adaptation, and heredity raises, he believes, strong probabilities against the inheritance of acquired characters. It is necessary to quote a few of his sentences.

(1) "Acquired characters are those which result from external influence upon the organism, in contrast to such as spring from the constitution of the germ."

(2) "Characters can only be inherited in so far as their rudiments (Anlagen) are already given in the germinal protoplasm (Keimplasma)."

(3) "Modifications which are wrought upon the formed body, in consequence of external influences, must remain limited to the organism in which they arose."

(4) "So must it be with mutilations, and with the results of use or disuse of parts of the body."

(5) "No such modifications of the body (affected by environment or by use and disuse) can be transmitted to the germ-cells, from which the next generation springs. They are, therefore, of no account in the modification of the species."

(6) "The only principle that remains for the explanation of the modification of the species, is direct germinal variation." "The intermingling of the sex elements is the origin of the variations on which natural selection in the usual way operates."

Weismann's position is thus clear and definite. The sole fountain of specific change is found in the germ-plasm of the sex-cells. The environment does make dints upon the organism, but only upon its body; the reproductive cells, through which alone the variation could be transmitted, are either unaffected or are not affected in such a specific way as to bring about the transmission of the acquired character. The effects of use and disuse may be marked enough, and important for the individual, but they are not transmitted, and therefore of no account in the history of the species. The ground is taken from under the feet of Lamarckians and Buffonians, and the whole burden of progress is laid upon germinal variation and natural selection.

Criticisms of Weismann's Position.

(1) Various naturalists have brought forward what appear to them to be examples of the genuine transmission of individually-acquired characters. Thus Detmer and Hoffmann among botanists, and Eimer among zoologists, may be quoted. The latter especially gives numerous examples to prove the untenability of Weismann's position. To some of the instances urged against him, Weismann has replied; but as each case has to be carefully tried on its own merits, and as sufficient decisive experiments

are still awanting, the matter lies beyond the scope of this historical sketch.

(2) Virchow has urged against Weismann what appear to him to be cases of the direct inheritance of climatic changes and pathological variations. But he appears to differ from Weismann in his definition of acquired characters, which, for the latter, do not include anything that can reasonably be traced back to a germinal variation. Ziegler has discussed the whole question of the inheritance of pathological characters, and comes to a conclusion harmonious with that of Weismann. Nor are the slow results of acclimatization good cases in the present discussion, since Weismann expressly allows that in long-continued conditions affecting the whole system the germinal cells may be directly affected along with, though not exactly by, the other elements of the organism.

(3) A criticism of a different nature has been suggested by several, but is well stated by Eimer. If the source of variation be restricted by hypothesis to the keimplasma intermingled in sexual reproduction, is this sufficient to account for the facts? "In what way, one must ask, have *new* characters first been introduced into the series? The sexual mixture could produce nothing; it could only work with what was already given." Professor M'Kendrick has forcibly emphasized a similar objection. There is no doubt, at any rate, that Weismann's theory, which excludes the direct assistance of environmental and functional variations, throws a still heavier burden than Darwin did on the shoulders of Natural Selection, which many believe to be already somewhat overweighted.

At the same time, it seems premature to conclude that the transmission of modifications is *impossible*, simply because we can find no proof of it, nor understand how it could be effected. In this connection it may be useful to recall a few general facts.

Every one allows the general conception of the various organs as symbions in a common life. We constantly speak of correlated variations, and though these generally work from the centre or germinal plasma outwards,

there is no *a priori* improbability against an environmental influence of some strength saturating through the entire organism, affecting one system by another, till eventually the reproductive cells share in the change. Weismann does not hold that the germ-plasm leads a charmed life in the symbiosis of the organism. It is not insulated from the general metabolism, in fact the germ-plasm may be stimulated to vary by nutritive changes. But to admit this is very different from admitting that a change in the body of a parent can so specifically affect the germ-plasm that a similar change, corresponding in direction though not in amount, is inherited by the offspring.

Apart from the general connectedness of the different parts of the body, and the common medium of the lymph and blood, it seems worth while to refer to the frequent occurrence of protoplasmic continuity within the system. In plants the intracellular connections by means of protoplasmic bridges are wide-spread; this is true in many cases in regard to the cells of animals. This is one of the various possible ways by which influences might pass from body to reproductive organs. That important influences, inciting change, pass in the opposite direction is well known. But it must be clearly understood that Weismann is quite willing to admit that changes in the body may stimulate the germ-plasm to change.

It is useful, also, to recall the numerous experiments which have been made on the determination of sex. Take only one example, the familiar case of Yung's tadpoles, where, by altering the quantity and quality of the food, he was able, for instance, to raise the percentage of females from the normal of about fifty to the abnormal of about ninety. Here, then, an environmental influence, playing in the first place on the nutritive system, saturated throughout the organism, and affected the reproductive system so as to swing the balance emphatically to the female side. General hypertrophy brought out of the primitive indifference an emphatic predominance of females. In this case the reproductive system was unquestionably reached, and

though the change that resulted was not, of course, one that was not in a sense implicit in the reproductive cells, it was none the less an alteration of the natural bias. Similarly, it is *possible* that very decisive functional and environmental modifications may saturate deeply into the organism, and affect the reproductive cells in such a definite manner that a tendency to change in the same direction may be transmitted to the offspring. But, as we have said, it is not justifiable at present to admit more than a possibility, and science does not deal with possibilities.

Filial Regression.

In his work entitled *Natural Inheritance* Galton was led by statistical methods to a very important generalization, which from one of its aspects may be called *the law of filial regression.*

A strange regularity is observable in the peculiarities of large populations throughout a series of generations. "The large do not always beget the large, nor the small the small; but yet the observed proportion between the large and the small, in each degree of size and in every quality, hardly varies from one generation to another." A specific average is sustained. And this is not because each individual leaves his like behind him, for this is obviously not the case. It is rather due to the fact of a regular regression which brings the offspring of extraordinary parents in a definite ratio nearer the average of the stock.

"However paradoxical it may appear at first sight, it is theoretically a necessary fact, and one that is clearly confirmed by observation, that the stature of the adult offspring must on the whole be more mediocre than the stature of their parents—that is to say, more near to the median stature of the general population. Each peculiarity of a man is shared by his kinsmen, but *on an average* in a less degree. It is reduced to a definite fraction of its amount, quite independently of what its amount might be. The fraction differs in different orders of kinship, becoming smaller as they are more remote."

As it is easy to misunderstand this important generalization, let us give some further illustration. It does

not hint at any depreciation of a good stock, for, as Galton shows, the offspring of two ordinary members of a gifted stock will not regress like the offspring of a couple equal in gifts to the former, but belonging to a poorer stock, above the average of which they have risen.

The fact of regression tells against the full transmission of any signal talent. Children are not likely to differ from mediocrity in a given direction so widely as their parents do in the same direction. "The more bountifully a parent is gifted by nature the more rare will be his good fortune if he begets a son who is as richly endowed as himself, and still more so if he has a son who is endowed more largely." But "the law is even-handed; it levies an equal succession-tax on the transmission of badness as of goodness".

Thus we reach the conception of the nation as a vast fraternity, with an average towards which the offspring of the extraordinarily gifted tend to sink, but to which the offspring of the under-average tend as surely to rise.

Galton's Law of Ancestral Inheritance.

We have noticed two great modern advances in regard to the problem of heredity—the doctrine of the continuity of the germ-plasm and the inquiry into the transmissibility of acquired characters, both closely associated with Weismann. To these we would add a third—Galton's law of ancestral inheritance. From data based on stature, the colour of Basset hounds, &c., Galton was led to a very important generalization, which he states as follows:—"Each parent contributes on an average one quarter, or $(0{\cdot}5)^2$, each grandparent one-sixteenth, or $(0{\cdot}5)^4$, and so on, and that generally the occupier of each ancestral place in the n^{th} degree, whatever be the value of n, contributes $(0{\cdot}5)^{2n}$ of the heritage". The law has been ably expounded and corroborated by Karl Pearson, who gives it an even more precise form.

There are still some difficulties to be met, but the formulation of the law is a great step, even if modifications should afterwards be necessary. As Prof. Pearson says: "the law of ancestral heredity is likely to prove one of the most brilliant of Mr. Galton's dis-

coveries; it is highly probable that it is the simple descriptive statement which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution be natural selection combined with heredity, then the single statement which embraces the whole field of heredity must prove almost as epoch-making to the biologist as the law of gravitation to the astronomer."

Chapter XII.

Palæontology.

Scope of Palæontology—Ancient Opinions—Mediæval Opinions—The Diluvial Theory—The Foundation of Palæontology—Cuvier—Lamarck—William Smith—Palæontology of Plants—The Cuvierian School—Richard Owen—Louis Agassiz—Palæontology after Darwin—Palæontology and Evolution.

Scope of Palæontology.

It is the task of palæontology to spell out the history of the past, so far as that can be deciphered from the fossil-bearing rocks, to trace the rise and decline of races, to disclose the sublime spectacle of life's progress. The palæontologist is no Dryasdust "poring over the entrails of an antediluvian frog", as a witty scholar once described him, he is rather one who makes the present intelligible in the light of the past. The palæontologists are the historians of the prehistoric, searching in the grave-yards of a buried past. For all practical purposes palæontology dates from Cuvier, who may be linked to the Victorian era, if we recall that Richard Owen, after studying in Edinburgh, went to Paris and listened to some of the famous anatomist's lectures. The study is thus strictly modern, but it may be of interest to notice briefly what was said about fossils in ancient days.

In ancient days there were four theories in regard to fossils.

(1) Some held them to be *lusus naturæ*, "sports of nature", of a mineral sort; and we do well to remem-

ber, that the long dispute as to the organic or inorganic character of *Eozoon canadense* has just ended at the close of the nineteenth century.

Ancient Opinions.

(2) The learned tell us, on the authority of Origen, that Xenophanes of Colophon, about 500 B.C., observed fossil fish remains in the rocks near Syracuse and Paros, and regarded them as remains of fishes which had been entombed when these parts of the earth were under water.

(3) Another characteristically ancient view, which both Aristotle and his pupil Theophrastus countenanced, though they did not wholly adopt it, was, that fossils were expressions of the earth's plastic virtue—results of spontaneous generation which had not succeeded in coming to the surface.

(4) The discovery of many hippopotamus bones in Sicily led Empedocles (about 450 B.C.) to regard this area as a battlefield between the gods and the Titans, and to interpret the bones as those of the *extinct* giants. Here the true idea of fossils glimmered for a moment, and was lost for much more than a millennium.

Mediæval Opinions.

It was in Italy, where shells abound in the rocks, that a revival of independent interest in fossils was first strongly marked. The artist and thinker Leonardo da Vinci, born in 1452, protested vigorously against the current traditional beliefs, maintaining that fossils were what they seemed to be—remains of animals which had once lived. In France, Da Vinci's common sense found a supporter in Bernard Palissy (1580), said to have been "the first to assert in Paris, that fossil shells and fishes had once belonged to marine animals".

The industrious accumulation of collections, and the cataloguing of these, began to make the traditional views less acceptable, but the truth had a slow dawn. Steno, a Dane, professor of anatomy in Padua, showed (1669) by actual comparison that the teeth of a living Mediterranean shark were identical with those found fossil in Tuscany, that fossil cockles and modern cockles had much in common, and made for the first time the suggestive observation that the oldest rocks contained

no fossils. He also reached many purely geological conclusions, and has been called, "the father and founder of the science". Similarly, Martin Lister, contemporary with Ray, and said to be the author of the first geological map, drew figures of modern shells and fossil shells side by side, noting in regard to the latter, "either these were terrigenous, or, if otherwise, the animals which they so exactly represent have become extinct".

Throughout the eighteenth century the dominant theory of fossils was that they were deposited by the Noachian flood, and a fierce campaign between orthodox and heretical science persisted for two generations. In 1726 Scheuchzer published his *Homo Diluvii Testis*, supposed to be a crowning proof of the diluvial theory. It contained a description of what was believed to be the skeleton of a child drowned by the Deluge, and it was not till long afterwards that Cuvier identified the interesting fossil as the remains of a gigantic salamander.

The Diluvial Theory.

We may close the pre-Cuvierian period with the illustrious name of Werner (1750–1817), who, according to his pupil Jamieson, was the first definitely to suggest that the different geological formations could be discriminated by their fossils, and that the newer the formation the more nearly do the fossils approximate to living forms. From this we see that the founding of palæontology was not far off.

The foundation of palæontology is usually placed, and with much justice, altogether to the credit of Cuvier, but it is historically truer to associate it also with Lamarck and William Smith. These three men, very different from one another,—the skilful anatomist, the evolutionary thinker, the English surveyor,—were complementary.

The Foundation of Palæontology.

In his study of the Tertiary mammals of France (1796) Cuvier turned his anatomical erudition and skill to good account, making absolutely clear for the first time that fossils were in most cases remains of extinct organisms, different from and yet

Cuvier.

related to modern forms. By his reconstructive genius and by his confident—sometimes over-confident—use of the principle of correlation, he brought the dead to life again, and insisted on their being ranked along with the modern types in a unified zoological system. He had clearly before him the central idea of palæontology, that of a succession of faunas upon the earth, and yet he lost the chief virtue of the idea by refusing to admit that the succession was genetic. It must be distinctly remembered that Cuvier believed in successive cataclysms which destroyed the population of each epoch and left the ground clear for a fresh creative act. Yet in Buffon's *Théorie de la Terre* he might have found a clear prevision of the anti-catastrophic or uniformitarian theory.

Lamarck (1744–1829).

Lamarck may be called the founder of the palæontology of the Invertebrate animals, not that he described even so large or so varied a collection as many of his predecessors, but because he studied them thoughtfully, and used his results in his pioneer work as an evolutionist. He studied in particular the fossil Molluscs of the Paris basin, showing that many were extinct, and that the different strata contained distinctive forms.

William Smith (1769–1839).

It seems, to say the least, doubtful whether the full import of Cuvier's work would have been so soon realized if there had not been the contemporaneous work of William Smith, who is often called "the father of English Geology". Independently of Werner he established the conception of a regular succession of strata in the earth's crust, showed that the various strata were definable by the fossils which they contained, and made the suggestive observation that the fossils were more divergent from the modern representatives the deeper or the older the strata in which they occurred.

Palæontology of Plants.

The study of fossil plants dates from the beginning of the nineteenth century, when Von Schlotheim (1764–1832), one of Werner's pupils, published what was probably the first illustrated volume devoted to the subject. Much more

important works by Sternberg, Cotta, Unger, Göppert, and others soon followed. Göppert is memorable for his experiments on the artificial fossilization of plants, which cleared up some obscured points, and for his discovery of the plant remains in coal.

Of great importance was Adolphe Brongniart's *Prodrome d'une histoire des végétaux fossiles* (Paris, 1828) and subsequent works, in which the author, following on Cuvier's lines, brought the past and the present together in mutual illumination. He was one of the first to outline the marvellous picture of the succession of "floras" upon the earth—the cryptogamic vegetation of the primary ages, the dominance of conifers and cycads in the secondary ages, the progress of angiosperms throughout the Tertiary times.

In England the palæontology of plants was for a time less enthusiastically prosecuted. Lindley and Hutton published in 1831–37 their three volumes on the *Fossil Flora of Great Britain*; Witham began the study of the minuter internal structure of fossil plants; and there were early contributions of importance by Hooker, Williamson, and others. To appreciate the present position of "phyto-palæontology" one must consult the botanical part of Zittel's great *Handbuch der Palæontologie*, or the works of Solms-Laubach and Saporta.

The Cuvierian School.

Even to name the workers of the Cuvierian school who raised palæontology to the dignity of being regarded not merely as auxiliary to geology, but as a distinct department of biology, is impossible within the narrow limits of this chapter, and would serve no useful purpose. We must restrict ourselves to keeping up the historical continuity by a note on two of the most outstanding representatives—Richard Owen and Louis Agassiz.

Richard Owen.

It may be said with fairness that the mantle of Cuvier fell upon Owen (1804–1893), for his indefatigable industry was for the most part devoted to analytic comparative anatomy; but it must also be recognized that under the Cuvierian mantle he wore, so to speak, part of the costume of Oken.

That is to say, he was a "philosophical anatomist", and believed that the facts of homology justified a doctrine of archetypal ideas. He differed from Agassiz most markedly in his apparent disregard of embryological work.

By his *Researches on the Fossil Remains of the Extinct Mammals of Australia, with a notice of the Extinct Marsupials of England* (2 vols., 1877), his *Memoirs on the Extinct Wingless Birds of New Zealand* (2 vols., 1879), his *History of British Fossil Reptiles* (1849–1884), his *British Fossil Mammals and Birds* (1846), his numerous papers on the Mesozoic land-reptiles to which he gave the name of Dinosaurs, his monograph on the oldest known bird, *Archæopteryx*, and a hundred other pieces of work, Owen did incalculable service to palæontology.

Sharing Cuvier's confidence in the principle of correlation, he did not hesitate to reconstruct from the most fragmentary evidence, and the mistakes into which he was thus often led have been valuable lessons to subsequent workers.

Louis Agassiz.

We have already noticed that Louis Agassiz (1807–1873) may be described as a Cuvierian who was at the same time an embryologist. His palæontological work, with which we have here to do, was mainly concerned with fossil fishes, to which he was attracted while still a young student, stimulated perhaps by Bronn's lectures on palæontology, by the publication of Goldfuss's *Petrefacta Germaniæ*, and by the fine collections of fossils at Munich. The precise opportunity for studying fishes was found, however, in a collection which had remained as a residue of a Brazilian exploration by Von Martius and Spix. These were handed over to Agassiz by Von Martius, who was professor of botany in Munich, and the coincidence is curious that one of Agassiz's subsequent explorations was to Brazil.

It is historically interesting to notice that as a student for a session in Heidelberg, Agassiz had attended the lectures of Schelling and Oken, which doubtless had their influence in strengthening his natural idealism.

As he says, the young naturalist of that day who did not share, in some degree, the intellectual stimulus given to scientific pursuits by physio-philosophy would have missed a part of his training. Another influence (at Munich) was that of Döllinger, an impressive master, at whose feet Von Baer also sat, and who probably inspired them both with the idea of the Recapitulation Doctrine, though Agassiz may also have learnt of this from Oken.

His industry as a student must have been like that of his later life, for he knew, he says, "every animal living and fossil" in eight museums in different German towns. One is hardly surprised to read that when Agassiz went to Paris to prosecute his work, Cuvier not only welcomed him, but handed over his drawings and notes on fossil fishes. The publication of the famous *Poissons Fossiles*, which extended from 1833 to 1844, involved extraordinary labour and self-denial on the author's part. In 1846 Agassiz migrated to America, where for twenty-seven years he exerted a profound influence both within and beyond zoology.

By his *Poissons Fossiles*, in which over a thousand species were recorded, most of them being described and figured, order was introduced into what had been chaos, and a magnificent demonstration was given of what anatomical patience and insight could do with subjects so difficult as many fossil fishes are. And although his classification according to scales cannot now be accepted for major groups, it must be remembered that the author was fully aware of its empirical character. As to the *basis* of classification, Agassiz was perfectly clear that there were three tests of a natural system: anatomical, palæontological, and embryological.

According to Eastman, Agassiz's work "marked an epoch in the history of palæontology and zoology in general, since one of its brilliant results was the discovery of certain comprehensive laws, which are now admitted to be of fundamental importance. Without doubt the most far-reaching of these in its consequences is the analogy which he pointed out between the em-

bryological phases of recent fishes and the geological succession of the class." Whereupon he deduced the generalization, "The history of the individual is but the epitomized history of the race". Another notable result was the recognition and characterization of his so-called prophetic or synthetic types, that is, such as embrace features in their organization which afterwards become distributed among a number of groups, and are never recombined.

Palæontology after Darwin.

Even after Lyell won conviction for his "Uniformitarian doctrine", for which Hutton had also contended, —that the earth has not been subjected to cataclysmic revolutions, but has been shaped and fashioned throughout the countless ages by processes not differing in kind from those which are at work to-day, the palæontologists still remained true to Cuvier, and antagonistic to Lamarck. There were indeed occasional suggestions of fresh light, but practically the dawn dates from Darwin (1859); and palæontology, like the rest of biology, felt the new influence.

"This revolution", Prof. Marsh says, "has influenced palæontology as extensively as any other department of science, and hence the new period. . . . In the last epoch, species were represented independently, by parallel lines; in the present period, they are indicated by dependent, branching lines. The former was the analytic, the latter is the synthetic, period. To-day, the animals and plants now living are believed to be genetically connected with those of the distant past; and the palæontologist no longer deems species of the first importance, but seeks for relationships and genealogies connecting the past with the present."

If any one man deserves to be put at the head of a department in science in modern times, Karl Alfred von Zittel (b. 1839) may be called the first palæontologist of the day. And this not only for his endless detailed researches, but because as a teacher he has influenced so many, by his living voice, by his text-books, and by his unrivalled arrangement of the palæontological collection at Munich. His great *Handbuch der Palæontologie*, of which he was editor and part author, occupied

him for eighteen years, and was completed in 1893. It stands alone as a compendium of palæontology.

Among the post-Darwinians there has been no more stimulating worker than Prof. Edward Drinker Cope (1840–1897), nor any whose work more strikingly illustrates the influence of the evolution-idea as an abiding thought. "Though, perhaps, often premature, and sometimes mingled with much error, which a more cautious inquirer would have avoided by waiting for additional evidence, his remarkable speculations—some have even dared to regard them as wild guesses—have had an influence on the progress of modern biological research which it is impossible to estimate."

His studies on fossil fishes and primitive vertebrates, on labyrinthodont amphibians, on anomodont reptiles, on extinct ungulates, and many more, stand out as monumental contributions to palæontology. The primitive mammal *Phenacodus*, a generalized type believed to have affinities with several of the orders of mammals, and with ungulates in particular, was one of his most interesting discoveries; while his "Tritubercular Theory", which traces back all the forms of molar teeth to a simple three-cusped or tritubercular type, may serve as an instance of his most successful morphological inductions. Osborn calls it "one of the chief anatomical generalizations of the present century".

Along with his friend Alpheus Hyatt, well known for his researches on the shells of extinct cephalopods, Cope founded the American school of Neo-Lamarckians. Palæontology seemed to him to furnish decisive proof of the inheritance of acquired characters, and to this belief in use-inheritance he added a theory, which has cropped up in many guises, that organisms were moved to vary by an inherent growth-force which he termed "bathmism".

Palæontology and Evolution.

Darwin himself insisted on the fundamental importance of palæontological facts as evidences of the Doctrine of Descent, and Huxley once said that if evolution had not already been an accepted theory, the palæontologists would have been forced to invent it. As with other depart-

ments of biology, so here we have to note that *mutual influence* of the ruling doctrine and the concrete investigations which has been so characteristic of progress in the Darwinian era.

On the one hand, the doctrine of evolution has given the palæontologists fresh inspiration and a new ambition. As Von Zittel puts it, "Palæontology has long ceased to place itself exclusively at the service of geology as the study of characteristic fossils. . . . To determine the genetic relationships, the ancestry, the modification, and the further development, in short, the race-history or phylogeny, of the organisms under consideration is now regarded as the essential, by many indeed as the chief aim of palæontology."

No one has dealt with the so-called palæontological evidences of evolution more forcibly, and at the same time more rigorously, than Huxley did, and it is very instructive historically to read his addresses to the Geological Society of London in 1862 and in 1870. In the former address he asked, "What then does an impartial survey of the positively ascertained truths of palæontology testify in relation to the common doctrines of progressive modification, which suppose that modification to have taken place by a necessary progress from more or less embryonic forms within the limits of the period represented by the fossiliferous rocks?" And his answer was, "It negatives those doctrines; for it either shows us no evidence of any such modification, or demonstrates it to have been very slight; and as to the nature of that modification, it yields no evidence whatsoever that the earlier members of any long-continued group were more generalized in structure than the later ones".

In the second address, eight years later, he gladly found reason to soften his "somewhat Brutus-like severity", while still insisting that "it is no easy matter to find clear and unmistakable evidence of filiation among fossil animals". "It is easy", he said, "to accumulate probabilities—hard to make out some particular case in such a way that it will stand rigorous criticism." As to the Invertebrates and lower Vertebrates, the evidence

still seems to him—the keenest champion the doctrine of evolution has ever had—very unconvincing; "but when we turn to the higher Vertebrata, the results of recent investigations, however we may sift and criticize them, seem to me to leave a clear balance in favour of the doctrine of the evolution of living forms one from another". It is probably safe to say that if he had given another address in 1890, he would have relented yet further.

On the other hand, the concrete investigations of palæontology continue to supply confirmation of the truth of the evolution-doctrine, though it must be frankly admitted that the so-called evidences are not *demonstrative* here or anywhere else.

Among the palæontological facts which are at once seen to be consistent with the evolution-idea, or even suggestive of it, two may be noted:—

(*a*) If we take differentiation and integration as standards of organic rank, we must admit that Fishes, Amphibians, Reptiles, and Birds are, as stated, in their natural sequence. But this is their order of appearance as fossils in the rocks. In other words, as the earth grew older, higher and higher types (as defined above) made their appearance. Of this there are many detailed illustrations. At the same time there are forms, like the Brachiopod *Lingula* or the mud-fish *Ceratodus*, which seem to have persisted with little change throughout countless ages, showing, as Huxley expressed it, that "progressive development is a contingent, and not a necessary result of the nature of living matter".

(*b*) A second set of facts may be described as the occurrence of fossil series. "In recent years", Von Zittel says, "a great number of closely-allied species have been traced through several superposed beds, stages, or divisions of formations, their exact morphological relationships have been studied in the most careful manner, and thus the probability at least has been established, that we are here dealing with a genealogical sequence of blood-relations. To be sure these do not as a rule form complete chains, wherein mutation is linked with mutation and species with species. They

are rather discontinuous series, of which all the members change in a definite direction, and obviously form steps in a line of development which culminates in the last-extinct or still-existing representatives." Zittel refers to such instances as the succession from *Hyracotherium*, or it may be from *Phenacodus*, through *Palaplotherium*, *Anchilopus*, *Anchitherium*, and *Hipparion*, to the single-toed horse. To this best-known instance might be added that of the camels, the pigs, the crocodiles, the amioid fishes, the ammonoids, &c. At the same time, it must in fairness be noted that the palæontologists remain in darkness in regard to many of the most momentous *origins* in the history of life. For what is really known as to the ancestry of Mammals, Birds, Reptiles, Amphibians, or Fishes, not to mention many an Invertebrate stock?

One of the most interesting and important of modern palæontological problems is whether there are chronological series of fossil embryonic types corresponding to the different stages in the development of a modern form. Is there palæontological evidence of that generalization which appealed so strongly to Agassiz though he was unable to see its evolutionary import—Hæckel's "Biogenetic Law". If this law be crudely and carelessly interpreted as implying an exact correspondence between individual and racial history, the answer must be an emphatic negative. As we have seen, careful embryological work points to the fact that the embryo, say of a fowl or duck, pig or rabbit, exhibits from a *very* early stage *individual* characters peculiar to fowl or duck, pig or rabbit—characters which date from the respective origins of these species. There is certainly no detailed or exact recapitulation, but this does not exclude the possibility that there may be fossil forms which bear a general resemblance to the youthful stages of modern forms.

"In spite of these drawbacks," Von Zittel says, "fossil embryonic types are not entirely awanting, even among Invertebrates. The palæozoic Belinuridæ are bewilderingly like the larvæ of the living *Limulus*; the Pentacrinoid larva of *Antedon* is nearer many fossil crinoids than is the full-grown animal;

certain fossil sea-urchins permanently retain such features as linear ambulacra and a pentagonal peristome, which characterize the young of their living allies; among Pelecypoda, the stages of early youth in oysters and Pectinidæ may be compared with palæozoic Aviculidæ. Among Brachiopods, according to Beecher, the stages which living Terebratulidæ pass through in the development of their arm-skeleton correspond with a number of fossil genera. Among completely distinct groups also, ontogenetic characters have been successfully traced. The beautiful researches of Hyatt, Würtenberger, and Branco have shown that all ammonites and ceratites pass through a goniatite stage, and that the inner whorls of an ammonite constantly resemble in form, ornament, and suture-line the adult condition of some previously existing genus or other."

But what the evolutionist would fain have from the palæontologist, what he wishes for much more than for "evidences of evolution", is some definite information as to the mode and method of organic progress. When we inquire, we find extreme difference of opinion, and no possibility of experiment to change theory into doctrine. To Cope the facts pointed clearly to use-inheritance; to Osborn this is, to say the least, doubtful; to others, there seems no evidence at all suggestive of such a conclusion. To some, the changes of structure observed in the fossil series seem clearly to indicate progressive variation in definite directions, but others point out that any proof of definiteness assumes the series of specimens to be fairly complete, or that we may have lost the initial stages before the indefinite variants were pruned off by natural selection. In short, as usual, we find interpretations where we require certainties.

As an illustration, however, we shall quote three conclusions from Prof. W. B. Scott's thoughtful and cautious essay on *Palæontology as a Morphological Discipline*.

(*a*) "Evolution is ordinarily a continuous process of change by means of small gradations" . . . "but this does not imply that a sudden alteration of conditions may not bring about discontinuity, or *per saltum* development."

(*b*) "Development is, in most instances, direct and unswerving. The rise of new forms, and the decadence and degeneration

of old ones, are not ordinarily by zigzag and meandering paths, but by relatively straight ones; and though, of course, a path once taken may be diverged from, yet in such a case it is not regained. This applies particularly to the organism as a whole; in minor details more latitude is permissible."

(*c*) "Parallelism and convergence of development are much more general and important modes of evolution than is commonly supposed. By parallelism is meant the independent acquisition of similar structures in forms which are themselves nearly related, and by convergence such acquisition in forms which are not closely related, and thus in one or more respects come to be more nearly alike than were their ancestors."

Chapter XIII.

Geographical Distribution.

Zoo-geographical Regions—Phyto-geographical Regions—Factors in Distribution—The Great Faunas and Floras: Littoral, Pelagial, Abyssal, Fluvial, Terrestrial—Evolution of Faunas.

Although various naturalists from Pliny to Buffon seem to have been impressed by certain outstanding facts concerning the geographical distribution of living creatures, the serious study of the subject hardly began before the Darwinian era. There was collecting of material and an occasional attempt to group plants and animals in geographical regions, but the significance of the problem could not be perceived without the light of the evolution idea. The main problem is to find out the causes of the existing distribution, to discover the factors which determine why certain organisms are here and not there, and others there and not here; but it is evident that the problem does not press upon the non-evolutionist.

Zoo-geographical Regions.

Following a short history of zoo-geography by Dr. Arnold E. Ortmann, we may distinguish various periods of inquiry into the regions of distribution.

A. Wagner seems to have been the first (1844–1846) to attempt any systematization of the mass of materials

which the explorers had accumulated. He divided the earth, in relation to the distribution of mammals, into a series of circumpolar zones. Louis Agassiz followed Wagner on similar lines (1845–1854). Dana was led by his studies on the distribution of corals to lay great, indeed exaggerated, emphasis on the (isocrymal) lines of equal minimum temperature in winter. In 1853 Schmarda distinguished no fewer than thirty-one continental and ten oceanic regions, but these were for the most part artificial. So far, only climatic and topographical determinants had been recognized, and even these with little clearness.

That little was achieved by these earlier workers must be admitted. Ideas were lacking; only two of the operative factors had been recognized; and even the descriptive survey was very partial. Ortmann cites Semper's verdict as to the state of affairs shortly before the publication of the *Origin of Species*. "Our whole zoo-geography is indeed nothing more than a great mass of materials thrown together without thought."

In 1858, however, Dr. P. L. Sclater published a fundamental paper on the geographical distribution of birds; in the same year Dr. A. Günther dealt with reptiles; but of even greater importance was the work of Andrew Murray (*The Geographical Distribution of Mammals*, London, 1866), who sought in the past history of the earth for a clue to the present distribution. The same note was struck by Jaeger and Bessels in their study of the distribution of deer; while Huxley, Semper, and others began to show the importance of considering the present state of affairs in the light of what was known as to relationships, pedigrees, and original head-quarters—thus introducing another new idea.

Prof. A. Agassiz's study of the distribution of the sea-urchins in four great realms may be noted as a very thorough piece of work in relation to a special group.

In 1876 Alfred Russel Wallace published his great work on the geographical distribution of animals, and gave a new dignity and stability to the whole inquiry. He did great service not merely by his systematic arrangement of an enormous mass of facts, but by

throwing the light of past history on the puzzle of existing relations, and by analysing the various limits of range, and the various modes of dispersal, which hinder or help the diffusion of organisms.

Since the publication of Wallace's book there have been many detailed studies of particular groups, *e.g.* of fishes by Günther; many detailed studies of particular regions, *e.g.* of the Philippines by Semper; and many criticisms relating both to the regions and the factors recognized by Wallace.

Phyto-Geographical Regions.

The study of the geographical distribution of plants began with Humboldt (1805), who not only described the peculiar "Physiognomik" of various regions, but sought an explanation of the peculiarities by reference to climate and soil —two undoubted factors which botanists have never ignored and have often exaggerated.

At the meeting of the British Association at Cambridge in 1845 Forbes directed attention to the importance of past geological changes, insulations, changes of level, &c., in relation to the distribution of plants.

Another important factor was indicated by Unger in 1852, who was the first to connect the present distribution of plants with that of previous ages as disclosed in the rock record. In 1855 Alph. de Candolle expounded the same idea, as Engler has also done in more recent years with conspicuous success.

As in regard to animals, so with plants, numerous suggestions have been made as to the mapping out of the earth, the various "systems", as they are called, differing from one another in emphasizing different factors.

Humboldt classified according to geographical zones and sea-level, and Meyen followed him in this simple method.

Schouw (1823) introduced a new idea of taking statistics as to the relative predominance of particular types in different areas, distinguishing the Cinchona realm, the Magnolia realm, and so on to the number of twenty-five, many of which have been confirmed as natural by subsequent workers.

About fifty years later, Grisebach (1872) admitted the evolution-idea, though without taking full advantage of it. Every species diffuses from its centre of origin, but is met by climatic and topographical limits, which have resulted in the local peculiarities now observable. Moreover, in the course of diffusion new species may arise in consequence of climatic change and spatial isolation.

The next great step was taken in 1882, when Engler, following Unger's lead, sought to connect the present vegetation with that of Tertiary times, and to show how the known differences might be definitely accounted for by known changes such as the Ice Age and changes of elevation. Drude (1884) also based his system on the past history of the plant world, but for the details he returned to Schouw's statistical method.

This brief retrospect shows that climate and soil, geological changes, topographical and other boundaries, means of dispersal, original headquarters and past history were gradually recognized as factors determining the present state of affairs. The difficulty is to combine them.

Factors in Distribution.

There is much scientific utility in an ordered map of the distribution of plants and animals over the earth and through the seas, but it would be a more valuable result if we could show how the present distribution has come to be. It is certainly instructive to note the resemblance in the fauna of areas so widely separated as Britain and Japan, the difference in the fauna of areas so near to one another as Florida and the Bahamas, or as Bali and Lombok (the two islands separated by "Wallace's line"), the distinctiveness of the Australasian fauna, the peculiarly discontinuous distribution of tapirs, Camelidæ, and Lemurs, and similarly in regard to plants, for these are among the outstanding facts of geographical distribution, but our standard of biological interest was greatly raised by Darwin. The real interest of the facts is only appreciated when we reach some solution of the factors.

Our knowledge of the factors is still incomplete, and

no one has yet given more than a very general account of the causes of the present distribution of plants and animals even in a small area like Britain; yet one step of progress is at least secure—it has been recognized that the result is due to the co-operation of many factors, and that any solution which does not recognize all the factors that are known is bound to be fallacious. The chief factors, which have been alluded to in the previous paragraphs, are: (1) the constitution of the organism; (2) the physical conditions of the region; (3) the position of the original headquarters of the stock; (4) the means of dispersal both active and passive; (5) the historical changes of the earth's crust and climate; and (6) the bionomic conditions which involve a struggle for existence.

The Great Faunas and Floras.

Although life is almost cosmopolitan, most of its forms have become adapted to particular conditions, and are more or less restricted to these. It is thus possible to make a much wider and more fundamental grouping than that into geographical realms; we may inquire into the distinctive population of the littoral, pelagial, abyssal, fluvial, and terrestrial areas (Lebensbezirke), and discuss their possible historical relations to one another. To this line of inquiry much attention has been directed of recent years, and although the problem is a fine instance of "reach exceeding grasp", many valuable results have already been gained.

Littoral.

By littoral we mean the area from high-tide mark to a depth of about 100 fathoms, where the plateau surrounding the continents ends. It is the smallest of the five chief areas in actual surface, but probably the richest in life. It includes a few flowering plants, *e.g. Zostera*, that can endure submergence, the great majority of the sea-weeds, and representatives of all the chief classes of animals except amphibians. From the time of Edward Forbes onwards much ingenuity has been expended in dividing the littoral area into zones in reference to the Algæ, the animals, or the nature of the substratum. It is an area of great physical variety, subject to continual vicissitudes, and much influenced

by diurnal and seasonal changes. It is the scene of an intense struggle for existence, and has been the happy hunting-ground of many of our greatest naturalists.

The lower boundary of the littoral area has been called the "mud-line", where the minute organic and inorganic particles derived from the land and surface waters find a resting-place, or form the food-supply of crowds of animals. Sir John Murray regards this line as "the great feeding ground in the ocean", and as the primary haunt from which animals migrated to the deep sea.

Pelagial.

The study of the fauna and flora of the open sea has not been long begun. For although the marvellous Johannes Müller, who found time for all sorts of researches, experimented about 1845 in "open-sea fishing with a fine net", and Eschscholtz was another pioneer, little was done before the *Challenger* expedition, and even then attention was mainly concentrated on the great depths.

From his *Challenger* experience Murray was led to conclude (1876) that there was an intermediate pelagic fauna between the surface and the depths. This was denied by Agassiz (1878, 1891) below 200 fathoms; but the later work of Chun (1888–1889) has confirmed Murray's conclusion.

A great step was taken by Hensen (1887), who improved the appliances, instituted a more systematic survey, and introduced the *quantitative method* of estimating the volume of floating organisms in different waters and at different depths, and the proportions in which different species occur. He is responsible for the term "Plankton", applied to floating organisms, and his theory of its uniformity over wide areas gave rise to a lively controversy between him and Hæckel, who strongly maintained its oscillating and extremely variable character. Improvement of plankton-methods, *e.g.* the use of the pump and self-closing tow-nets (still far from practical perfection), their application to lakes and even rivers (*e.g.* by Zacharias); the taking of observations at different seasons throughout the year; and a combination of zoologists and botanists in the

task, have already greatly increased our understanding of the "metabolism of the ocean", as Hensen expressed his ultimate aim.

Abyssal.

One must not forget the pioneer work of Wallich, Carpenter, and others, but our knowledge of the abyssal fauna practically begins with the *Challenger* expedition.

The researches of the *Challenger* and analogous expeditions have made it certain that there is no depth-limit to the distribution of animal life, that there are in the great abysses representatives of most of the classes from Protozoa to fishes, and that the distribution of some types tends to be cosmopolitan in correspondence with the uniformity of the physical conditions.

As to these physical conditions, the deep-sea world is in darkness, apart from occasional "phosphorescence", for a sensitive photographic plate is not influenced below 250–500 fathoms; the temperature is about freezing point, the heat of the sun being practically lost at about 150 fathoms; the pressure is enormous, about 2½ tons per square inch at 200 fathoms; the cold water in sinking brings down a relatively large proportion of oxygen; it is quite calm, for the effects of the greatest storms are only felt near the surface.

There are no plants, apart from the resting stages of a few doubtful algoid forms, for typical vegetable life is dependent upon light, and not even bacteria, otherwise so omnipresent, are known to occur in the great depths. The animals feed on one another and on the organic debris which sinks down from above.

Modern research has yielded no result more stimulating to the imagination than the tidings of this strange, silent, cold, dark, plantless world and its numerous inhabitants.

The *Challenger* and subsequent expeditions yielded results which have been worked up in many of the leading biological laboratories of Europe and America, and there is now an abundance of reliable data; not enough, however, to settle some of the most interesting questions which the facts raise.

What of the metabolism of deep-sea animals, the

influence of their peculiar environment on their ordinary functions, and on their growth and reproduction? There is little but analogy to suggest an answer, and it does not follow that what is deduced from experiments (by no means numerous) will hold true of organisms which have been habituated to their environment for many millennia.

There is a marked resemblance between the Arctic and Antarctic abyssal fauna Is this resemblance thorough-going,—is it primary? or is it the secondary result of migration to and fro along the bottom?

How far are the observations numerous enough to warrant conclusiveness of statement as to the uniformity which some speak of, and the localized distribution which the *Challenger* statistics tend to prove?

What of the origin of deep-sea animals? Was there any truth in Sir Wyville Thomson's theory of the existence of an abyssal fauna from Palæozoic times? or is Sir John Murray altogether right in his view, that the deep-sea fauna has been the result of migrations from the region of the mud-line in relatively recent times?

Fluvial.

We may, perhaps, use the term fluvial to include fresh-water areas, whether they be lakes or ponds, rivers or streams; and although observations on their tenants are as old as the naturalist, we must again record that the systematic study of fresh-water faunas and floras is of very recent date. The biological station over which Prof. Zacharias presides at the great lake of Plön has been an example to the biological world, and the hint has been taken in America and elsewhere, though Britain lags discreditably behind. There are interesting practical problems in connection, for instance, with fishes and water-supply; and there are yet more interesting theoretical problems in connection with adaptation, migration, and origin.

Some clearness has been introduced by distinguishing, as may be done in regard to other life-areas, four sets of tenants: (*a*) the recent immigrants, *e.g.* the bivalve *Dreissenia* from the sea; (*b*) the relics which have been left behind as survivors of the inhabitants of

an ancient sea, *e.g.* many of the molluscs of Lake Tanganyika; (*c*) the cosmopolitan forms which are readily transported on birds' feet and otherwise from one water-basin to another; and (*d*), if any remain, the autochthonous or aboriginal forms which are not represented by any near relatives outside of fresh water.

The question of the origin of land animals was present to the inquiring minds of the Greek philosophers, but, so far as we know, it has not been seriously tackled except by one naturalist, Prof. H. Simroth, in his *Entstehung der Landthiere* (1891). And notwithstanding the author's ingenuity and learning, the work does not convey the impression of a problem solved.

Terrestrial.

Slowly, and it may have been by zigzag paths, organisms wandered inland from the shores of sea and estuary and river, or became able to survive the drying up of landlocked basins. Simroth seeks to show that hard skins, cross-striped muscle, brains worthy of the name, red blood, and so on, were acquired as the transition to terrestrial life was effected.

Besides the five main life-areas—littoral, pelagial, abyssal, fluvial, and terrestrial—minor ones might be distinguished. Much work of interest has been recently done in regard to the organisms found in brackish water, in caves, underneath the ground, in the air, within other organisms, and so on. But to discuss these is beyond our scope.

It is at least stimulating to think over the possible historical relations of the great faunas which we have alluded to above. Various possibilities may be stated.

Evolution of Faunas.

(*a*) According to Moseley, "The fauna of the coast has not only given origin to the terrestrial and freshwater faunas, it has throughout all time, since life originated, given additions to the pelagic fauna in return for having received from it its starting-point. It has also received some of these pelagic forms back again, to assume a fresh littoral existence. The terrestrial fauna has returned some forms to the shores, such as certain shore-birds, seals, and the polar bear; and

some of them, such as the whales and a small oceanic insect, *Halobates*, have returned thence to pelagic life.

"The deep-sea fauna has probably been formed almost entirely from the littoral, not in the most remote antiquity, but only after food, derived from the debris of the littoral and the terrestrial faunas and floras, became abundant in deep water.

"It was in the littoral region that all the primary branches of the zoological family tree were formed; all terrestrial and deep-sea forms have passed through a littoral phase, and amongst the representative of the littoral fauna the recapitulative history, in the form of series of larval conditions, is most completely retained."

(*b*) According to Professor W. K. Brooks and others, the primitive fauna was pelagic. From this have been derived the tenants of the shore and of the deep sea. To the latter, however, he does not deny the possibility of ascending again. The relative easiness of life in the open sea and the unlimited supply of simple Algæ are especially suggestive in connection with this theory.

(*c*) According to Professor A. Agassiz, Prof. H. Simroth, and others, if we may venture to compress their views into a sentence, a littoral fauna was the original one, whence have been derived, on the one hand, the pelagic and abyssal faunas, and, on the other hand, the fresh-water and terrestrial faunas.

(*d*) Sir John Murray has emphasized the importance of the mud-line as, at any rate, important headquarters of animal life, and as the area from which wanderers have sunk down to the great abysses.

Chapter XIV.

Bionomics.

The Term Bionomics—History of Bionomics—Fritz Müller as a Type—Organisms and their Environment—Adaptations—Sprengel—Nutritive Chains—Inter-relations between Plants and Animals—Inter-relations among Animals—Inter-relations among Plants—The Struggle for Existence.

The Term Bionomics.

When we think of the life of a man, our first thoughts are usually of his active relations with the world around him, of his family and friends, of his endeavours and achievements; and it is in most cases only as a second thought that we inquire into the functioning of his heart or digestive organs. For it seems convenient, if not logical, to distinguish between the internal activities of the body and the wider life in which the man comes into active relations with his fellows, with other living creatures, and with the inanimate world.

So it is with the life of plants and animals. There is the internal life of the body, and there is the wider external life of inter-relations with other individuals and with the world. For the study of this wider life a term is needed, and various suggestions have been made.

Professor E. Ray Lankester, in his article "Zoology" in the *Encyclopædia Britannica*, proposed the term Bionomics, defining it as "the lore of the farmer, gardener, sportsman, fancier, and field-naturalist, including Thremmatology, or the science of breeding, and the allied Teleology, or science of organic adaptation: exemplified by the patriarch Jacob, the poet Virgil, Sprengel, Kirby and Spence, Wallace, and Darwin".

It has been said that Bionomics is merely a learned word for "natural history", but this has already a heavy burden to bear; it has been translated "life-history", but this has a more definite meaning already; it has been called "higher-physiology", but this,

though logical, would provoke misunderstanding; the Germans often use the word biology in the sense of Bionomics, but this is confusing; some suggest "the study of external relations", but all vital functions have external relations. So far as we know, the only other expressive term is that of *Œcology*, which Hæckel proposed in 1869, defining it as comprising "the relations of the animal to its organic as well as to its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes into direct contact . . . those complicated mutual relations which Darwin designates as conditions of the struggle for existence".

History of Bionomics.

It is not possible to say much in regard to the historical development of this line of biological research, for it rarely acquired either dignity or definiteness until Darwin demonstrated its importance. In fact, one of the greatest debts which biology owes to Darwin is, that he gave new meaning to Bionomics.

It is true that since animate nature first claimed the intelligent interest of the observer, there have been those who were more strongly attracted to the study of habits, behaviour, and inter-relations than to any other aspect of life, yet their interest was oftener emotional than intellectual, and the real import of their study was unperceived. Thus, though Gilbert White, author of *The Natural History and Antiquities of Selborne*, was prototype of the better class of modern amateurs, and in such observations as those on earthworms (1777) was a worthy predecessor of Darwin, he can hardly be said to have been aware of the wider import of his studies on habit.

Buffon may perhaps be called the greatest of the pre-Darwinian students of Bionomics. He had all the attributes of a philosophic naturalist, and deliberately set himself to a study of the habits of animals and their adaptations to their environment. This gives a particular interest to his *Histoire Naturelle*, which may be described as an eighteenth-century analogue of Brehm's *Thierleben*.

Before Darwin's day the student of habits, interrelations, and adaptations had been looked upon by his sterner brethren with more or less contemptuous indulgence.

Since Darwin's day, however, the study of bionomics has risen to worth and dignity, though there are still some who misunderstand its merits. (*a*) It is plain, in the first place, that it must be a very incomplete biology which does not take account of the living creature. The bird's song is nothing to the morphologist, except in so far as the anatomy of the syrinx or song-box is concerned, but it is nevertheless an essential part of our biological conception of the songster, and it cannot be understood apart from other songsters. (*b*) Throughout organic nature—in plant and animal—we find adaptations of structure, many of which are only intelligible when we consider the organism in its relations to its animate and inanimate surroundings. Whatever be our theory of the origin of adaptations, many of them have no meaning if we leave the organism isolated or unrelated. (*c*) The modern conception of life has as one of its central ideas the efficacy of natural selection or elimination in the struggle for existence; it is plain that if we are to judge justly of this it can only be by seeing its actual (not fancied) operation in particular cases. (*d*) The study of bionomics supplies much of the raw material of the incipient science of comparative psychology. (*e*) And finally, if there be any vision more than another which stimulates the mind of the biologist it is the peculiarly Darwinian vision of an infinite web of life, of a vast system of linkages binding part to part throughout the world—the conception of the correlation of organisms.

Fritz Müller as a Type.

We have Darwin's authority for taking Fritz Müller (1822–97) as a type of the modern naturalist, and it would be difficult to find another in whom the characteristic features of the Darwinian era reached a finer development. A few personal details, taken from Hæckel's "Appreciation", may be used to illustrate the scientific temper of the man, and also, we believe, of many modern students of bionomics.

Fritz Müller's father, grandfather, and great-grandfather had been pastors, but there was a strongly-marked scientific bent in the family, which cropped out also in Fritz's younger brother Hermann, famous for his work on the fertilization of flowers. It is also interesting to notice that Fritz Müller was one of the many students who sat at the feet of Johannes Müller and were inspired by his genius.

His conscientious scruples against taking the Protestant oath, necessary in order to become an "Oberlehrer", led him to emigrate to Brazil in 1852, and he never returned. He settled for four years on the outskirts of the primitive forest in the valley of Garcia, observing and collecting indefatigably. Then followed twelve years at the Lyceum of Desterro [literally "banishment"] in the island of Santa Catharina, off the coast of Brazil, where he investigated the marine fauna and wrote his famous *Facts for Darwin*. Ousted from this post by Jesuit influence (1867) he retired to Blumenau, and spent twenty years in what might be called scientific Walden-life. The Emperor of Brazil, Don Pedro II., appointed him (1876) naturalist to the national museum at Rio Janeiro, where many of his collections had been sent, but even this modest post was soon lost (1884) by the short-sighted tyranny of a political reaction. Offers of pecuniary aid from his admirers in Germany were gratefully but firmly declined, and the "prince of observers", as Darwin called him, resolutely adhered to his plain living and high thinking. From his hermitage he continued to send home the records of his observations, which remain a lasting monument to his enlightened patience and critical insight.

Fritz Müller's work was chiefly concerned with what are now called the problems of bionomics. In other words, he was pre-eminently an observer of the web of life, of the inter-relations of living creatures. His papers deal with the struggle for existence in the tropical forest, with the mutual adaptations of plants and animals, with leaf-cutting ants and myrmecophilous trees, with mimicry and protective resemblance, with

the division of labour among the Termites,—in short, with the detailed working of natural selection.

Philosophically a Monist, biologically a Darwinian, he was above all an observer, distrusting theories, and always sounding the note of objectivity, as we would expect from one who lived and thought looking nature straight in the face.

Until biology becomes as different from what it is now, as the biology of to-day differs from that of the pre-Darwinian era, Fritz Müller will be remembered for his *Für Darwin*, and for his studies in the bionomics of Brazil, *i.e.* for his detailed application of Darwinism, on the one hand, to the class of Crustaceans, and, on the other hand, to the facts of life in the primitive Brazilian forest. Apart from the Recapitulation Doctrine, which is at present so much in the fire that judgment must be suspended, Fritz Müller made two personal contributions which are of great importance. The one is his modification of the theory of mimicry; the other is a contribution to the theory of variation, which is often referred to under the title of "Müller's law".

To abstract the plant or animal from the particular *milieu* in which it lives is like trying to understand man apart from society.

Organisms and their Environment.

On the one hand, we see the organism's action upon its environment,—the nitrifying, sulphur-making, decomposing work of bacteria; the weathering caused by lichens; the protective action of littoral sea-weeds, bog-mosses, grass, and trees; the accumulations of peat and coal; or, among animals, the slow formation of ooze on the floor of the sea, the making of coral-reefs, the agricultural work of earth-worms and termites, the destructive effects of boring animals; and so on through a long list illustrating the hand of life upon the earth. As distinctively modern, we might cite the researches of Darwin on earth-worms, of Drummond on termites, of Darwin, Murray, and others on coral-reefs. Very characteristic, too, are the numerous researches by which bacteriologists have convinced us that it is no metaphor to speak of the living earth.

On the other hand, and of more biological importance, there is the action of the environment upon organisms. This formed the main subject of Prof. Karl Semper's masterly Lowell Lectures in 1881, and his book should certainly be ranked first in the literature of the subject. If we add to that the records of a representative series of experiments, such as those of Professor Weismann on the seasonal dimorphism of butterflies, of Professor Poulton on the coloration of caterpillars, of Dr. De Varigny on the dwarfing of water-snails (*Limnæus*), of Profs. Born and Yung on the determination of sex in tadpoles, and similar experiments by M. Maupas and Prof. Nussbaum on the rotifer *Hydatina senta*; and finally read Prof. Weismann's Romanes Lecture, we gain a fair idea of the present state of knowledge and opinion on the subject.

As the result of much detailed work, biologists have become clearer as to the complex relations between organisms and their environment. A summary may be attempted here.

(1) There is the relation of normal functional dependence, in virtue of which life continues from moment to moment, as may be illustrated by the respiratory interchange of gases. Of the same sort, obviously, is the relation between the developing embryo and its environment, including not only the essential food-supply, but various external stimuli, such as gravity, pressure, the chemical medium, heat, light, and electricity.

(2) There is the relation of direct modification, wherein an environmental change produces a change in the metabolism of the organism which is followed by a lasting change of structure. There must always be *some* change of structure, but if this passes what may be called *the limit of vital elasticity* the result is a "modification" which persists. The Lamarckians believe that these modifications of the body may affect the germ-cells in such a way that the offspring may show a change in the same direction as the original modification, and apart from the recurrence of a similar environmental influence. This remains a hypothesis, and there are few facts at present known which can be said to favour it.

(3) The environment seems sometimes to give the organism what may be called a variation-stimulus. An environmental change may "let loose" a constitutional, congenital, or germinal predisposition to vary in a given direction, or it may stimulate germ-plasm to vary in some new way, the result being manifest in the next generation.

(4) Environmental changes (topographical, climatic, &c.) impose or remove restrictions on distribution and on the range of possible pairing among the members of a species. In other words, the relations of organisms and their environment include isolation and dispersal.

(5) There is the relation of elimination, wherein the environment operates unequally on the members of a species, killing some and sparing others, shortening the life of some and lengthening that of others, inhibiting the reproduction of some and favouring that of others, which is one aspect of the struggle for existence.

Adaptations.

Perhaps the most far-reaching word in biology is this word adaptation or fitness. The idea it expresses is familiar to all. Everyone knows of associations of men—whether firms or societies, universities or families—in which the component members pull well together, and are, or become, mutually adapted. Similarly with plants and animals; there is internal adaptation of organ to organ, as of bone to muscle; there are adaptations of the organism to its inanimate surroundings, as the cactus to the desert; there are adaptations of organism to organism, as the flower to its favoured insect-visitors, and the insects to their favourite flowers. The study of bionomics is in great part concerned with these adaptations.

Sprengel.

In discussing sex and reproduction in plants, we have briefly noticed the pioneer work of Christian Konrad Sprengel (1750–1816), but he cannot be left out of a chapter on bionomics.

After being ejected from the rectorate of Spandau for neglecting his flock in favour of flowers, he settled down to a frugal life in Berlin, and gave lessons in languages and botany. A back room at the top of a lodging-house was filled with his herbarium, his books,

and tobacco smoke; . . . he walked for half a day without rest even when an old man; . . . on Sundays he usually conducted botanical excursions which any one might join on payment of two or three groschen. . . . "On these occasions", an old pupil says, "he explained equally well the inscription on a tombstone, the construction of a windmill, the course of the stars, or the structure of a plant . . . the commonest plant became new by what he had to say about it; a hair, a spot, gave him opportunity for questions, ideas, investigations."

The life-work of Sprengel was expressed in his now famous book *The Secret of Nature discovered in the Structure and Fertilization of Flowers* (1793), which gives a detailed account of his observations on the flowers around Berlin. He showed that most of the flowers have nectar, and he interpreted the colour as an advertisement of this, suited to catch the insect-eye. By the insects' visits pollination is secured, which is important, since self-pollination is often impossible—for various reasons, but especially because of a want of time-keeping (dichogamy) between the stamens and pistil of a given flower. But there is no detail of the flower without its meaning: variously coloured spots serve as honey-guides or pathfinders to the exploring insects, hairs protect the nectar from rain and yet offer no obstacle to desirable visitors, other arrangements secure that the insects are dusted with pollen; such was the tenor of this pioneer's interpretation, all in a manner with which Darwin and his successors have made us familiar. If Sprengel had only discovered the *utility* of cross-fertilization, which Darwin proved experimentally, his work could hardly have been overlooked as it was.

The Secret of Nature seems to have fallen quite flat, probably because little interest was at that time taken in such inquiries, partly perhaps for extrinsic reasons, such as the unpopularity and unconventionality of the author. At all events, for nearly seventy years after its publication this bionomical classic was unjustly forgotten. In 1841 it came into Darwin's hands, and

impressed him as being "full of truth", although "with some little nonsense". And at last Sprengel's work had its reward.

Nutritive Chains.

Of much importance in the understanding of the relations between large sets of organisms living in the same area, is the occurrence of what may be called "nutritive chains". As Prof. O. Zacharias points out, some of the fresh-water fishes in a pond depend upon the supply of small crustaceans (copepods, &c.), and these again on much minuter organisms (infusorians, diatoms, &c.), and these again, to some extent, on the bacteria which cause the putrefaction of the dead organic matter. In short, there is a circulation of matter from one level of life to another.

Dr. Bernhard Fischer has shown that even on the high-seas bacteria are present, playing their usual part of "middlemen between death and life" by transforming dead organic matter into inorganic substances which can be used again by plants. As far as is known they are absent from the ice-cold water on the floor of the ocean.

Prof. W. C. M'Intosh and Mr. George Murray have given definiteness to the conclusion that "all fish is diatom" in the same physiological sense as "all flesh is grass". The food-canals of the copepods, and other small crustaceans which form a large part of the food of fishes, contain abundant remains of the siliceous shells of diatoms.

Inter-relations between Plants and Animals.

There is not a more fascinating chapter in bionomics than that which deals with the inter-relations of plants and animals. We refer to their complementary relations as regards interchange of gases with the atmosphere; the ultimate dependence of animal-life upon plant-life, since only plants can subsist upon inorganic food; the selective action of animals on plants, which Prof. Stahl has worked out in the case of snails; the selective action of bacteria on animals, which Prof. Haycraft has skilfully dealt with in connection with man; the carnivorous plants, which have fascinated many from Linnæus to Darwin; the whole question of the pollina-

tion of flowers by insects; the problem of galls; the symbiosis of Algæ and Radiolarians; and a hundred other inter-relations. A convenient introduction to the subject will be found in the writer's *Study of Animal Life* and in Prof. Geddes's *Chapters in Modern Botany*.

Inter-relations among Animals.

It is again to Darwin that we are most indebted for our realization of the now familiar biological fact that no animal lives or dies to itself. We refer to such facts as the following:—the existence of quaint partnerships, as of crocodile and crocodile-bird; the closer "commensalism" illustrated by certain hermit-crabs and their companion sea-anemones; the frequent occurrence of parasitism; the establishment of complex domestic and social relations; and the manifold adaptations which may be called "shifts for a living", such as mimicry and masking.

As a particular example we may refer to the investigations of Dr. Wasmann, M. Charles Janet, and others on the "myrmecophilous" animals, *e.g.* small beetles, which live along with ants, and in their varied relations present a close parallel to the animals found in a human dwelling; some are distinctly unwelcome, others are simply tolerated, some are useful, others are mere "pets".

Inter-relations among Plants.

The modern recognition of the fundamental physiological resemblances between plants and animals was a momentous step in the history of biology; the recognition of their bionomical resemblances is hardly less important. The struggle for existence between plants in the tropical forest or in the hedgerow; the many degrees of parasitism of plant upon plant; the living together or symbiosis which is illustrated in the combination of Alga and Fungus to form a Lichen, and so on, are instances of inter-relations among plants which have their parallels in animal life.

If we study Kerner's *Life of Plants*, or Wiesner's *Biologie der Pflanzen*, or a similar work by Ludwig; if we read Rodway's account of death in the tropical forest or Gardiner's sketch of the struggle for existence in a meadow; if we consult Schimper on myrmecophilous

plants or Lündstrom on the little shelters (domatia) which various trees offer to useful mites,—we gain the impression that even the general life of plants is not very different after all from that of animals. This, as it seems to us, is the greatest result of the modern study of the bionomics of plants.

The Struggle for Existence.

Although the idea of a struggle for existence is very ancient, expressed, for instance, by Empedocles, Aristotle, and Lucretius, it remained little more than a general impression until Darwin and Wallace showed not only its reality, but how it may operate as a factor in evolution. Both of these naturalists have referred to the work of Malthus as one of the sources of their inspiration, and it has been pointed out by Prof. Geddes that the biological emphasis on struggle is entirely congruent with the keen competitive conditions of an industrial age.

The colour of Darwin's picture of nature certainly suggests a very keen and continuous struggle for existence. He speaks of "the battle for life" and "the severe, often recurrent struggle". "In a state of nature, animals and plants have to struggle from the hour of their birth to that of their death for existence." On the other hand, it should be carefully observed that Darwin used many saving-clauses. Thus, in speaking of the struggle for existence, he says, "I should premise that I use this term in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny". Similarly Mr. Wallace says, "The struggle for existence, under which plants and animals have been developed, is intermittent and exceedingly irregular in its incidence and severity".

The reality of the struggle is beyond all doubt, but there remains a lack of statistics and analysis without which even the biologist can hardly escape from platitudes. We require to have some measure of the intensity of the struggle in actual cases, and a more careful distinction between its different modes. It is obviously unsatisfactory that the important generaliza-

tion, that the struggle is most severe between closely-allied forms should not be more carefully substantiated than it usually is. Darwin gave some half-dozen examples, not all of which are correct. The necessity for the struggle depends upon: (*a*) the tendency of organisms to rapid increase; (*b*) the variability of the physical environment, to which organisms are at best only relatively well adapted; and (*c*) the secondary consequences of these primary facts; but it is the unfulfilled duty of the student of bionomics to accumulate a mass of precise evidence.

It is plain that the nature of the struggle must vary greatly with the nature of the organism; thus that of the beech-tree must be very different from that of the squirrel. It is plain that the phrase includes at least three different forms of struggle: with related fellows, with foes, and with inanimate nature. The objects of competition include (1) continued individual existence and well-being, and (2) the continuance of family and kin—both of them objects of great complexity. It is also a familiar fact that the struggle varies in intensity with the rate of reproduction and with the variability of the environment. Thus we reach the conclusion that *the struggle for existence is a function of numerous—partly dependent, partly independent—variables.*

Taken literally, the "struggle for existence" seems somewhat too strong a phrase to use in describing the pursuit of such luxuries as a seventh wife, or that continuous endeavour after well-being which ensures a few years longer life to the stronger constitution. But even when the phrase is literally appropriate, we must remember the altruistic colouring of many facts of life—attraction between mates, reproductive sacrifice, parental and filial affection, the kindliness of kindred, gregariousness and sociality, co-operation and mutual aid.

Observation shows us what we are tempted to call mere physical attraction between cells which are at the same time entire organisms. In some types of simple many-celled animals, and in most plants, the attraction remains cellular, being confined to the sex-cells. Gradually there appears, as we ascend the animal series, a

sexual attraction of entire organisms. When we find a centralized nervous system developed, we may speak of two organisms being in varying degrees aware of one another. The awareness is by and by accompanied by a reflex of emotion, the creatures seem to be fond of each other. Various æsthetic attractions are added to the primary ones, and, on a long inclined plane, "love" emerges. At the same time, however, there has evolved a parento-filial affection, and it is easy to understand how "love", broadened in the family, returns enhanced to the pair. And along with this there is also the evolution of a sense of kinship, which is expressed in mutual aid.

Our point is simply that sexual attraction, kinship, altruism, and love (or whatever names be given to their pre-human analogues) are important facts and factors in life, which must be taken account of in connection with the struggle for existence. This has been said many times by Spencer, Darwin himself, Fiske, Geddes, Kropotkine, Drummond, Coe, and others.

Just as Empedocles recognized two ultimate forces—love and hate,—so Spencer has insisted on recognizing altruism as well as egoism in nature. "If we define altruism as being all action which, in the normal course of things, benefits others instead of benefiting self, then, from the dawn of life altruism has been no less essential than egoism. Though primarily it is dependent on egoism, yet secondarily egoism is dependent on it." "Self-sacrifice is no less primordial than self-preservation."

From another side the conception of the struggle for existence has been modified in post-Darwinian days. It has been deepened by a recognition of the struggle of parts within the organism;—the struggle of organs, tissues, and cells; the idea is verifiable in the history of ova and spermatozoa; and Weismann has suggested its application to the behaviour of the minute particles which compose the germ-plasm.

When we bear in mind (*a*) the great variety of cases in which the phrase cannot be literally used; (*b*) the great number of cases in which there is no direct com-

petition, *e.g.* in the reaction of solitary animals to a change of environment; (*c*) the manifold facts of life to which some such word as altruism must be applied; and (*d*) the applicability of the general idea to parts within the organism, or to such processes as the race of many spermatozoa towards one ovum, we recognize that the phrase "struggle for existence" must be taken as a technical expression of what occurs whenever the effectiveness of an organic response is of critical moment in relation to continuance, welfare, and evolution.

In other words, the broadening and deepening of the idea of struggle—one of the features of post-Darwinian biology—leads us to recognize that progress depends on much more than a squabble around the platter; that the struggle for existence is far more than an internecine struggle at the margin of subsistence; that it includes all the multitudinous efforts for self and for others between the poles of love and hunger; that it comprises all the endeavours of mate for mate, of parent for offspring, of kin for kin; that love and life are factors in progress as well as pain and death; that life for many an animal means the well-being of a socially-bound or kin-bound organism in a social *milieu*; that egoism is not satisfied until it becomes altruistic.

Chapter XV.

Psychology of Animals.

Biology and Psychology—Theological Interpretation—Metaphysical Interpretation—Animal Automatism—The Word "Instinct"—The Inclined Plane of Activities—Lamarckian Theory of Instinct—Darwin's Position—The Work of Romanes—Weismann's Position—Lloyd Morgan's Experiments—Open Questions—Psychological Aspects of Mating.

From early times men have interested themselves in what may be called the mental life of animals, but, excepting Descartes, there was little attempt at scientific

treatment before the Darwinian era. In fact, the problems of the psychical life of animals were in most cases deliberately left alone by many of the most competent pre-Darwinian biologists, who pretended to regard them either as quite outside their province, or as altogether beyond solution. Not a little of this assertion of "intellectual preserves" still remains. Of late, however, biologists have begun to rescue the subject from the credulity of the amateur and the frequent dogmatism of the philosopher. This has been prompted partly by the recent advances in regard to the physiological aspects of human psychology, and partly by the development of the evolution-theory, which has not only convinced us of the unity of nature, but has directly raised many psychological questions. A discussion of Darwin's theory of sexual selection, for instance, necessarily demands some psychological analysis, as Darwin himself recognized by his work on the *Expression of the Emotions*.

Biology and Psychology.

Following Prof. Groos, we may distinguish a theological, a metaphysical, and a more or less consistent scientific stage in the history of opinion in regard to the mental life of animals.

The theological mood found a short and easy method of getting rid of all difficulties by leaving the mental life of animals directly in the hands of the Creator. Of that as an ultimate statement the scientific investigator has no criticism, for he himself ventures no ultimate explanations; it amounts, however, to a refusal to consider the problem scientifically, and it is to be feared that this sort of piety has often served as a cloak for intellectual indolence.

Theological Interpretation.

H. S. Reimarus, a shrewd observer, who published a large work on Instincts in 1760, may be taken as an early representative of theological interpretation; and Romanes quotes a typical sentence from Addison: "I look upon instinct as upon the principle of gravitation in bodies, which is not to be explained by any known qualities inherent in the bodies themselves, nor from any laws of mechanism, but as an immediate impression from the first mover and the divine energy acting

in the creatures". So strongly was this view engrained that attempts at analysis were frowned upon as materialistic or irreligious, and Groos notices that fear of the Sorbonne's disapprobation led Leroy to publish his famous *Letters on Animals* as if from "a physician of Nuremberg".

Closely allied to the theological interpretation is that of various metaphysicians who have interested themselves in the psychological aspects of animal life. Thus Schelling, who had a strong influence on German biology, said that "animals in their works and ways were but expressions or instruments of the universally immanent reason, without being themselves reasonable. Only in what they do is there reason, but not in themselves." Of this position, too, there are modern representatives, for instance, E. von Hartmann, who, while perfectly aware of the suggested scientific interpretations, finds satisfaction in none, and falls back upon his metaphysical principle of "the Unconscious".

Metaphysical Interpretation.

The extreme of reaction from metaphysical interpretation is to be found in the Cartesian doctrine that animals are automata. As Huxley has told us, Descartes was an unwearied dissector and observer, "a physiologist of the first rank", who did for the nervous system what Harvey had done for the heart and blood-vessels. He recognized that the brain was the organ of mental processes, that muscular contraction is (usually) dependent on nervous stimuli, that there are sensory and motor nerves, that reflex actions may take place without volition or even contrary to it, and he held an almost modern theory of memory.

Animal Automatism.

Starting from reflex actions in man, co-ordinate and purposive, though unwilled and unconscious, Descartes argued that animal activities might be of a similar nature, though doubtless requiring in most cases a more refined and complicated nervous mechanism. As Huxley puts it, almost quoting, as he points out, from Malebranche's statement of the Cartesian doctrine, "what proof is there that brutes are other than a

superior race of marionettes, which eat without pleasure, cry without pain, desire nothing, know nothing, and only simulate intelligence as a bee simulates a mathematician?"

"I desire", Descartes said, "that you should consider that these functions (including mental processes) in the machine naturally proceed from the mere arrangements of its organs, neither more nor less than do the movements of a clock or other automaton, from that of its weights and its wheels; so that, so far as these are concerned, it is not necessary to conceive any other vegetative or sensitive soul, nor any other principle of motion or of life, than the blood and the spirits agitated by the fire which burns continually in the heart, and which is in no wise essentially different from all the fires which exist in inanimate bodies."

Could Descartes have known, as we do, the results of experiments on the brain and nervous system, the observations on the life of those who have suffered serious nervous injury through wounds or disease, the researches on the hypnotic and related states, or even the phenomena of chloroforming, he would doubtless have been even more convinced than he was as to the truth of his theory of animal automatism. And yet there are few who would now accept it!

The strongest argument against Descartes' position is an indirect one, which we owe to the evolution-idea—the conviction of unity and continuity in nature. We cannot for a moment believe that conscious experience began in man. "We know", Huxley says, "that, in the individual man, consciousness grows from a dim glimmer to its full light, whether we consider the infant advancing in years, or the adult emerging from slumber and swoon. We know, further, that the lower animals possess, though less developed, that part of the brain which we have every reason to believe to be the organ of consciousness in man; and as, in other cases, function and organ are proportional, so we have a right to conclude it is with the brain; and that the brutes, though they may not possess our intensity of consciousness, and though, from the absence of language, they

can have no trains of thoughts, but only trains of feelings, yet have a consciousness which, more or less distinctly, foreshadows our own." In short, the theory of "animal automatism" violates our conception of continuity in evolution. Either the one or the other must be sacrificed.

Historically, the Cartesian theory had but a limited influence, much less, indeed, than it deserved. Erroneous though we must believe it to be, it was more in the line of progress than the metaphysical interpretations which outlived it.

The Word "Instinct".

While it may be possible for us to appreciate the theological and metaphysical interpretations, and to see them in perspective as complementary, not antagonistic, to scientific analysis, the historical fact must be recognized that they tended to hinder research. The observer watched the industry of bees, birds, and beavers, pronounced the word "Instinct", and turned away to something which seemed more intelligible. "Instinct" was regarded as an inborn gift defying all analysis. It was cited, even by Hume, as an ultimatum, like life itself. Others compared it to gravitation.

But this easy-going—and in reality quite unprogressive—way of looking at the facts could not last. On the one hand, the critics began to show that many cases of alleged instinctive activity were really cases of rapid learning. Thus Alfred Russel Wallace pointed out that birds hatched and brought up alone do not build the characteristic nest, nor sing the characteristic song of their kind. He argued justly that imitation, education, and individual intelligence count for much, and that the sphere of instinct had been grossly exaggerated. On the other hand, the critics pointed out that instinctive activities were not so stereotyped or perfect as was generally supposed. In fact, as Büchner, Vogt, and others showed, instincts might sometimes lead the animal astray. For a time, however, verbal discussions as to "instinct" seem to have been even more rife than the disputes of economists as to the meaning of "value".

As human psychology became more precise, as careful and critical observations on animal activities increased in number, and as reflex actions began to be generally understood, the idea of arranging vital activities in a series became clearer.

The Inclined Plane of Activities.

Beginning at the top, we recognize some *rational* activities in ourselves,—activities which we cannot explain psychologically without postulating general ideas. Whether it be making an engine or guiding an empire, the activity implies certain abstract conceptions, or conceptual inferences.

On a distinctly lower plane are ordinary *intelligent* actions which demand inferences but not necessarily abstract ideas. To cultivate one's garden cannot be the whole duty of man, as the French philosopher maintained, for while it demands intelligence it does not necessarily cultivate reason. So far as we know, the animal does not rise above this level of intelligence, or perceptual inference, or concrete judgment. That is to say, the most brilliant illustrations of animal intelligence may be explained psychologically as involving perceptual but not conceptual inference, concrete but not abstract judgment. If we allow the cogency of the logical law of parsimony we must abide by the simplest adequate hypothesis. This is the position of those who allow that animals have intelligence, but maintain that man has a monopoly of reason. But this has no meaning unless a definition of the terms, as above indicated, be agreed upon.

It is well known, however, that activities originally demanding intelligent control may in the individual lifetime become *habitual*. Being often performed, they bring about, it is supposed, a modification of cerebral structure, the establishment of "habit-tracts", as some would say; at all events, there is no doubt that they become habitual, whatever that may exactly mean.

Now, beginning at the lower end of the scale, we recognize in our own life some very simple *automatic* activities whose psychical side is unknown, such as the physiological rhythms of the heart and lungs, which go on without conscious control, and without external

stimulus other than that of the persistence of the essential conditions of life.

Slightly higher are the *simple reflexes* which may be performed without the co-operation of the higher brain-centres, and are also independent of conscious control. Swallowing and sneezing are familiar examples.

Higher still are *complex reflexes*, illustrated especially in often-repeated activities which were never under intelligent control. These are habitual, but they have a different origin from the habitual-intelligent activities above referred to. According to many, the instincts of ants and bees, for instance, are nothing more than very complex reflexes, but it is doubtful whether we ever get quite near enough to them to detect the individual variations which may give them intelligent (as well as instinctive) character.

In the middle of this inclined plane between habitual-intelligent activities and complex reflexes we may place instinctive activities. They differ from habitual-intelligent activities in being inborn or innate, requiring no experience nor education, though they are often perfected thereby. They are also shared by all the members of the species in almost the same degree, and biologically they are of critical moment in the struggle for existence. They differ from complex reflexes in involving the activity of the higher nerve-centres, and it is probable, though not exactly demonstrable, that they are associated with consciousness.

Our metaphor of the inclined plane emphasizes the probability that there are no hard-and-fast lines separating the different grades of activity from one another.

The theory of instinct which was dominant before Darwin's day may be conveniently termed Lamarckian.

Lamarckian Theory of Instinct.

It interpreted instincts as the outcrop of inherited habits. By "lapsing of intelligence", as G. H. Lewes termed it, activities which originally demanded intelligent control may become habitual, and it was supposed that in the course of generations these habits might become engrained in the constitution; in short, inheritable. Similarly, complex reflex actions becoming habitual might also give

origin to instincts. The main drawback to this Lamarckian theory is the absence of evidence that acquired characters may be inherited, but this difficulty was usually slurred over until Weismann's essays made this easy-going procedure impossible.

Darwin's Position.

Darwin recognized a twofold origin of instincts. On the one hand, he admitted the possibility of the Lamarckian interpretation:—Habits are established; cerebral changes ensue; it may be that the inheritance of these is the explanation of some instincts. But it cannot be the explanation of all, he said, for every one knows that the non-reproductive worker-bees and worker-ants have instincts which are quite foreign to their parents—the males and queens. Thus, there must be another explanation of instincts, and this Darwin found in the action of natural selection on *congenital* variations.

The Work of Romanes.

One of the most prominent names in the history of animal psychology is that of George John Romanes (1848–1894), for, although there is legitimate difference of opinion as to the cogency of some of his conclusions, he did more perhaps than any other to raise the subject into dignity, and to place it on a secure biological basis. He approached the study from two sides, as a physiologist and as an evolutionist, for his earlier work was concerned, on the one hand, with the nervous and locomotor activities of medusæ, star-fishes, and sea-urchins; and on the other hand, with a critical study of Darwinism. In his first published work dealing with animal psychology (*Animal Intelligence*, 1881) he set forth the reliable data, partly from his own observation, largely from those of others, and sifted the precise from the anecdotal. In his *Mental Evolution in Animals* (1883) he developed his theory of instinct, distinguishing *primary* instincts, which arise, apart from intelligence, in the course of natural selection, and *secondary* instincts, which arise by the habituation and inheritance of activities originally intelligent. In the same volume he began the comparison of the mental life of man and animals, which he further developed in a third work on *Mental Evolution in Man* (1888).

As Professor Lloyd Morgan says, "by his patient collection of data, by his careful discussion of these data in the light of principles clearly and definitely formulated, by his wide and forcible advocacy of his views, and above all by his own observations and experiments, Mr. Romanes left a mark in this field of investigation and interpretation which is not likely to be effaced".

When Weismann, aided by Galton and others, ran the doctrine of Use-inheritance to earth, and showed, at least, that it was an illegitimate postulate until definite evidence was forthcoming, the supporters of the Lamarckian theory of instinct began to recant. Thus, A. Forel, famous for his observations on ants, says, "I formerly believed, as others did, that instincts were inherited habits. I am now convinced, however, that this is an error, and have accepted Weismann's conclusion. Indeed, one cannot see how a truly acquired habit, as in piano-playing or bicycle-riding, can transmit its mechanism to the germ-plasm of the offspring." In 1883 Weismann distinctly committed himself to the conclusion that all instincts have their roots in germinal variations. Following Darwin, he showed how difficult it was to give a Lamarckian interpretation of such cases as the nuptial flight of the queen-bee, which occurs but once in a lifetime, or the slave-keeping instincts of some sterile worker-ants.

Weismann's Position.

As in other departments of biology, so here, the only way of escape from the muddy quagmire of verbal dispute and the will-o'-the-wisps of irresponsible speculation is the way of experiment. The most notable pioneer on this path is Professor C. Lloyd Morgan. Following the old experiments of Spalding, and influenced perhaps by the new movement in human psychology towards experimental work, Mr. Lloyd Morgan set himself to observe young chicks hatched in an incubator, away from all taint of parental education or possibility of imitation. He afterwards extended his observations to other birds. It is plain that this is the only method of precisely determining what powers are really born in the creature, and much success has attended his investigations. Mr.

Lloyd Morgan's Experiments.

Lloyd Morgan's works on *Animal Life and Intelligence*, *Comparative Psychology*, and *Habit and Instinct*, cannot be too strongly recommended to the student of the mental life of animals.

Open Questions.

The first task of the inquirer is to make sure of the data, to distinguish observation from inference, to sift out precise evidence from the carelessly anecdotal, and to give prominence to cases in which some simple experiment was used to check the impressions of the observer. The second task is to give the simplest psychological interpretation that is adequate to cover the facts. Although there is still great room for improvement, it must be allowed that there has been of recent years marked progress in regard to both accuracy of observation and criticism of interpretation.

With the data before him the naturalist has then to inquire into the psychological interpretation, and there are three questions which are naturally raised by each case. (1) Is the behaviour such that, if it occurred in man, its psychological aspect could be legitimately expressed without postulating general ideas, abstract reasoning, or conceptual judgment? Does it imply intelligence, or more than that—reason? It may be safely said that the majority of naturalists who have given attention to the subject are agreed in the conclusion that there are no certain cases of animal behaviour which necessitate the assumption of a conceived, as contrasted with a perceived purpose.

(2) A second question is, whether the instance of animal behaviour under discussion shows any sign that the creature is utilizing its individually acquired experience, or is modifying its mode of action in reference to what it has learned, or in relation to some quite novel situation. If this question be answered in the affirmative, then one must allow that the animal is in such behaviour *intelligent*. And of this there are endless illustrations among the higher animals. On the other hand, if the behaviour, however marvellous and effective it may be, does not show profiting by experience nor adaptation to quite novel ends, the probability is that

the activity is *instinctive*. Of such activities Lloyd Morgan's general description is as follows:—"Instincts are congenital, adaptive, and co-ordinated activities of relative complexity, and involving the behaviour of the organism as a whole. They are not characteristic of individuals as such, but are similarly performed by all like members of the same more or less restricted group, under circumstances which are either of frequent recurrence or are vitally essential to the continuance of the race. While they are, broadly speaking, constant in character, they are subject to variation analogous to that found in organic structures. They are often periodic in development and serial in character. They are to be distinguished from habits which owe their definiteness to individual acquisition and the repetition of individual performance."

There is general agreement that the term "instinctive" and not "intelligent" covers the greater part of the more complex activities of the lower animals, such as ants, bees, and wasps. When Bethe (1898) answers in the negative the question—"Is it permissible to ascribe psychical qualities to ants and bees?" and concludes from his experiments that these insects are only "reflex-machines", he is simply using new (and not improved?) terms to indicate the old distinction between intelligent and instinctive.

In many cases it seems necessary to make a compromise, and to interpret certain activities as in part intelligent and in part instinctive. Often it appears as if the animal went jogging along instinctively, pursuing a beaten track in obedience to its inherited cerebral mechanism, but suddenly a novel emergency arises, and such intelligence as the animal has seizes hold of the reins of life.

(3) A third question at present divides comparative psychologists into two camps. Given a case which all will agree to regard as instinctive, *e.g.* the comb-building of bees, the problem at once arises as to the *origin* of this instinct. Modern progress has consisted in practically reducing the alternative theories to two. The instinct is either the outcome of the inheritance of

the results of experience accumulated in former generations (Lamarck, Spencer, Wundt, &c.); or it is the outcome of congenital variations wrought upon in the usual way by natural selection (Weismann, Ziegler, &c.).

(4) There remains a fourth question practically unanswerable at present:—Excluding intelligence, by hypothesis, what degree of consciousness attends the performance of instinctive actions? Does an instinctive action rise to the *focus* of consciousness, or is it, as it were, on the *margin* of consciousness, or is it wholly *subconscious*? As yet we are hardly warranted in having more than mere opinions on the subject.

As an illustration of what may be called distinctively post-Darwinian work, we may take Prof. K. Groos's study of the play of animals. Unless we choose to regard nature as an illusion, we must admit that many animals play, as really as children do. The simplest forms of play are concerned with bodily movements, and may be described as gambols and frolics; also very fundamental is the game of experiment in which the animal without serious purpose tests things, itself, or its fellows; and from these roots arise more complex forms of play, the sham-hunt, the race, the sham-fight, and so on.

The first interpretation of the play of animals was due to the poet Schiller, and was afterwards independently elaborated by Herbert Spencer. According to this theory, play is an expression of superabundant vitality, of overflowing energy, of irrepressible good spirits. But this merely states one of the internal conditions of play, and does not interpret the quite distinctive forms of play observed in different kinds of animals. Nor does it fit in well with the familiar sight of a dog or a child turning in a moment from extreme weariness to riotous play. Spencer eked out the theory by suggesting that while surplus energy was the fundamental condition, the precise forms of play were defined by *imitation*. But although imitation is of enormous importance in life, it does not explaim the forms of play; we need only recall the play of animals, *e.g.* kittens, which have been isolated in early life.

According to Groos, play is the outcrop of instincts which have been evolved like other instincts, arising by congenital or germinal variation, and fostered in virtue of their utility. But what can be the utility of play, which by definition has no serious purpose?

To this Groos answers that play is of fundamental importance as "the young form of work". The play period is an apprenticeship, a preparation for adult life, with the great advantage that mistakes are not of serious moment. Throughout the ages those kittens and other young carnivores which hunted best in fun have hunted best in earnest; the non-players and the bad players have been eliminated. Play is thus a rehearsal without responsibilities, a sham-fight before the battle of life begins, a preliminary canter before the real race. In short, as he says, while there is some truth in the assertion that animals play because they are young, it is perhaps as true that they have a period of youth in order that they may play, and the forms of play have been defined in relation to the realities of adult life.

A second justification of play is found in the simple fact that it affords opportunity for the exercise and perfecting of instinctive activities, which, therefore, do not require to be so definitely engrained in the cerebral constitution. Thus, it may be said that play is a device which lightens the burden of inheritance.

It is certainly a suggestive idea that the play-period affords scope for the rise and progress of new variations before the struggle for existence has become keen. It affords what the Germans call *Abänderungs-spielraum*—elbow-room for initiatives, new departures, idiosyncrasies, which form the raw material of progress. The importance of this biological justification of play in relation to human children is obvious.

Psychological Aspect of Mating.

There are few great facts of life in regard to which precise observation and critical interpretation would be more welcome than in regard to animal courtship. Here, even in spite of himself, the biologist must become a psychologist. The historical aspect of the question admits of brief statement. (*a*) Long before Darwin's day, naturalists

had observed the courtship of animals, and had concluded that the female often *chose* a mate from out of a number of rival suitors. Thus Bechstein concluded that the hen-bird often selected the best singer as her mate. (*b*) Darwin generalized the facts in his theory of sexual selection, according to which many secondary sex characters have been evolved through preferential mating, the females choosing one male rather than another, and that not whimsically, but in relation to definite qualities, without which the male tended to remain unmated. "If it be admitted", he said, "that the females prefer, or are unconsciously excited by, the more beautiful males, then the males would slowly but surely be rendered more and more attractive through sexual selection." As Lloyd Morgan tersely puts it, "the hypothesis of sexual selection, stripped of all its unnecessary æsthetic surplusage, suggests that the accepted mate is the one that most strongly evokes the pairing instinct". (*c*) Then followed what may be called the biological criticism of the theory of selection. Thus Wallace and others pointed out that there was insufficient evidence to show (*a*) that the females did really choose, or (*b*) that even the most unattractive males remained unmated,—the two most important postulates of the theory.

(*d*) Within recent years a more exact psychological study of mating has got under way, though it has not advanced far beyond the stage of asking questions. To what extent are the courtship activities instinctive? How far is their definiteness sustained by tradition? Is there any evidence of what might be called intention in the dances and songs, the parades and displays of the males, or is it all the expression of periodical fits of exuberant gladness and uncontrolled emotional ecstasy?

Here one needs to consider the modern theory of emotions as due to visceral changes, evoked by external or internal stimuli, which affect the brain through afferent nerves, and are associated with motor impulses which determine their external expression. If the dance, the song, and the like are regarded as expres-

sions of sexual emotion, "such expression may have *suggestive value*, and serve to evoke an answering emotion. In this case the act of pairing would be correlated with the expression of sexual emotion through certain specialized activities; and those individuals which were not expressive, together with those which were insensible to the suggestive influence of expression, would be less ready to mate and to transmit the specialized modes of expression" (Lloyd Morgan).

(*e*) Groos has suggested a way of looking at the facts which well deserves consideration. Since the sexual instinct is obviously, in most cases, of extraordinary strength, it is in the interest of race-preservation that its satisfaction should be kept within bounds. In relation to this we find that a long-continued preliminary excitement is often necessary. In particular, the instinctive coyness of the female has to be overcome. And it is in reference to this end that the often elaborate courting instincts have been evolved, *i.e.* in the course of natural rather than sexual selection.

Chapter XVI.

Evolution of Evolution-Theory.

The Evolution Idea—Greek Period—Mediæval Period—Scientific Renaissance—Philosophic Evolutionists—Speculative Evolutionists—Pioneers of Modern Evolution-Doctrine—Darwinism—Conflict of Opinions—Some Recent Steps—Conclusion.

The Evolution Idea.

The general idea of organic evolution—that the present is the child of the past—seems to be almost as old as the earliest records of clear thinking. It is in great part just the idea of history—of human history—projected upon the organic world, but it is differentiated by the qualification that the continuous "becoming" had been wrought out by forces inherent in the organisms themselves and in their environment. In other words, evolution is a *natural* history.

But simple as the idea is, it has been slowly evolved, gaining content as research furnished fuller illustration, and gaining clearness as criticism forced it to keep in touch with facts. It has slowly developed from the stage of suggestion to the stage of verification; from being an *a priori* anticipation it has become an interpretation of nature; and from being a modal interpretation it has advanced to the rank of a causal theory.

Almost all naturalists now accept the Doctrine of Descent, here wisdom is certainly justified of her children; but it is quite another thing to be ready with a Theory of Evolution. In short, the *fact* of organic evolution forces itself upon us, but a study of the *factors* is still a lesson in uncertainties.

Greek Period.

In estimating the guesses at truth which abound in the writings of the early Greek philosophers, we must avoid two opposite errors,—on the one hand, that of reading into them a scientific value which they are far from possessing; on the other hand, that of unduly depreciating them because they were imaginative, not inductive.

Thales (624–548 B.C.), the Ionian, was one of the first to suggest the theory that all things arose from water, a theory, as Professor Osborn remarks, natural "in a country surrounded by warm marine currents prodigal with shore and deep-sea life"; Anaximander (611–547), the Milesian, had some crude notion of metamorphoses, and forestalled the grotesqueness of some modern versions of Recapitulation in his picture of the emergence of ancestral man from an encapsuled fish-like stage wafted ashore like a mermaid's purse; Anaximenes (588–524) had a theory of a primordially prolific earth-slime, which seems like a far-off suggestion of one of Oken's dreams.

We reach firmer ground when we pass from the earliest schools to those who are often called the Physicists. Heraclitus (535–475) held a vividly kinetic conception of the universe, as a system of continuous movements, a view as familiar to the Greek mind as it is in modern physics, and perhaps furnishing one of the elements which went to the composition of the evolution

idea. Empedocles (495–435), whom Osborn calls "the father of the evolution idea", pictured the gradual origin of diverse forms—first plants and then animals—through the chance play of the combining force of love and the separating force of hate upon the four elements—fire, water, earth, and air. The first forms, being monstrous failures, were eliminated and replaced by more successful though still fortuitous products of Nature's spontaneity. Here we find a glimmering of the idea of the survival of the fittest or natural selection. Democritus (450 B.C.?), famous as an early materialist and perhaps the first comparative anatomist, recognized the general occurrence of fitness, even of single structures and organs, but he does not seem to have had any theory of its origin. He advanced some views in regard to heredity, which are usually spoken of as suggestive of pangenesis. Anaxagoras (500–428), on the other hand, was the founder of teleology, in so far as he began to invoke the aid of intelligent design to separate out and arrange the germs of life which existed from all time in the air or ether.

Even when the pre-Aristotelian philosophers condescended to statements with some direct relation to facts, it is difficult for us at this distance of time to understand how much they really meant. But there is little of this difficulty in regard to Aristotle, who combined in equal excellence the qualities of philosopher and naturalist, and, far ahead of his age, made the transition from guess-work to induction. He held the idea of a gradual progression in nature from the inorganic to the organic, and from one grade of life to another. As to the factors in this progression, he does not seem to have worked out the problem concretely; he refused the suggestion that adaptive structures could be the result of the elimination of the unfit, and believed that "nature produces those things which, being continually moved by a certain principle contained in themselves, arrive at a certain end". He expounded the doctrine of a "perfecting principle" or "physical formal cause" which struggled with the "physical material cause" or matter itself, and worked out a continuous and progressive

adaptation—an idea which has often recurred in the minds of evolutionists, but which seems to await adequate exposition in the hands of some other supreme combination of philosopher and naturalist.

Mediæval Period.

The foundations so firmly laid by Aristotle remained almost unbuilt upon till the scientific renaissance at the end of the sixteenth century; only here and there did some strenuous worker raise a corner a few feet higher; often, indeed, the outline of the whole was obscured by rubbish. There were, however, two important influences which should be borne in mind—the influence of the fathers and schoolmen, and the influence of Arabic science.

Within the church there were two movements which are still discernible—that of the literal and that of the liberal party. The literalists may be represented, for instance, by such "an extreme conservative" as the famous Spanish Jesuit Suarez (1548–1617); they reacted against Aristotelianism, and held firmly to the *ipsissima verba* of the Mosaic cosmogony. The liberal party, represented, for instance, by Augustine (353–430), and in extreme form by Bruno (1548–1600), were wisely content to define creation as the institution of the order of nature, and some of them found no difficulty in combining with this a more or less clear acceptance of evolution-ideas.

Among the Arabs science found, for a time, an environment more congenial than Europe afforded; it was there that the Aristotelian tradition was kept most vigorously alive, it was there that his works were first translated (between 813 and 833), and accepted as a treasure to be traded with, not merely hidden in a napkin and buried in the ground. Avicenna (930–1037) expresses the "culmination of Arabic science", but, after a period of glimmering, the light failed.

Scientific Renaissance.

Towards the end of the sixteenth century, under a variety of potent influences, science reasserted itself as a natural development and discipline of the human spirit, and, in the vigour of conscious youth, threw off the cramping bonds of a warped Aristotelian tradition, and put away the childish things with

which mediævalism had amused itself. Men passed surely, though slowly and imperfectly, from hearsay and tradition to observation and experiment, from imagining to induction. During the earlier period of this renaissance, inquiry was so thoroughly pre-occupied with the observed facts of nature that little attention was paid to the problem of evolution; thus, before we reach any great evolutionist who was at the same time a concrete naturalist we find (*a*) a school of philosophic evolution, (*b*) an abundance of somewhat rank and random speculation, and (*c*) a number of fruitful concrete suggestions in anatomy, physiology, and embryology, which were not connected into a system.

Philosophic Evolutionists.

Prof. Osborn notes the striking fact "that the basis of our modern methods of studying the evolution problem was established not by the early naturalists, nor by the speculative writers, but by the philosophers. They alone were upon the main track of modern thought." It must be remembered in this connection that many of these philosophers reaped the reward which never fails those who turn with independent minds to Aristotle and Plato, and that many of them were expert students in some department of natural science.

Francis Bacon (1561–1626), for ever famous for his insistence on the true method of scientific inquiry—by observation, experiment, and induction—may be noted here as one of the first to apprehend the possibility of the transmutation of species by accumulated variations, and to propose, what is not even yet realized, an Institute of Experimental Evolution. René Descartes (1596–1650) was the Bacon of France, noteworthy for his appreciation of the idea of gradual development and for his daring attempt to explain the universe on physical principles. In regard to both, however, he was fatally inhibited by the orthodox dogma of special creation. Gottfried Wilhelm Leibnitz (1646–1716) is memorable for his doctrine of continuity—that all natural orders of beings present but a single chain, along which advance is made by degrees and never by leaps, as the existence of intermediate species clearly shows. The idea of evolu-

tion is also expressed by Spinoza and Hume, by Lessing and Schelling, and by Kant and Herder. And Hegel was nothing if not an evolutionist.

The title "Speculative Evolutionists" is borrowed from Prof. Osborn's history, to include a variety of writers who yielded to the vice of unverified speculation. Speculative Evolutionists.

We need not go further back than Benoît de Maillet (1656–1738), the author of *Telliamed*. He believed in the rapid transformation of organisms by changed surroundings and habits, and in the transmission of the resulting modifications, but he discounted even his premonition of Lamarckism by deriving birds from flying-fishes and man from the mermaid's husband.

Of greater interest are the suggestions of the mathematician Maupertuis (1698–1759). He distinctly stated a pangenetic theory of heredity, as in the words "The elementary particles which form the embryo are each drawn from the corresponding structure in the parent, and conserve a sort of recollection of their previous form, so that in the offspring they will reflect and reproduce a resemblance to the parents". He supposed that fortuitous variations might arise by the diversified arrangement of the elementary particles, and anticipated an even more modern doctrine in the suggestion that new species might be physiologically isolated by being sterile with other members of the stock.

Diderot (1713–1784) proposed a theory of gradual development from pre-existent germs, and, as Mr. Morley and Prof. Osborn point out, revived the idea of the survival of the fittest which Empedocles had so long before suggested. It is also very interesting to find that he thought of the particles of the organism as striving through many failures to attain stable combinations,—a far-off hint of the modern conception of the struggle of parts.

Charles Bonnet (1720–1793) was driven by the failure of his eyesight from valuable observations, *e.g.* on the parthenogenesis of Aphides, to somewhat profitless speculation. He is well known as the author of the term "Evolutio", which he applied, however, not to

the history of the race, but to individual development. Influenced by Leibnitz's law of continuity he held the conception of an "échelle des êtres", unbroken even by death, and linking all forms of life from the lowest to the highest, a conception in which Prof. Geddes sees a reflection of ecclesiastical hierarchy, and Prof. Osborn an adumbration of the immortality or continuity of the germ-plasm. As to the unrolling of the chain throughout the ages, Bonnet believed, like Aristotle, in an internal perfecting principle, and saw in adaptation simply the realization of a predetermined harmony.

J. B. René Robinet (1735–1820) was also under the influence of Leibnitz, and supposed a continuous chain of being from stone to man. But he had not even the root-idea of evolution, for the various links of the chain were regarded not as a genetic series, but as the direct products of germs with which nature was supposed to experiment in her continual efforts after greater perfection.

Lorenz Oken (1776–1851) was a follower of Schelling, and therefore careless as to the inductive method on which the substantiation of science must always rest. If we collect his best passages a case may with some difficulty be made out for regarding him as a pioneer of modern biology; if we attend to his absurdities we are forced to regard him as a fatuous follower of intellectual will-o'-the-wisps. He found the hypothetical origin of organisms in a primitive slime (*Ur-Schleim*) which had its cradle on the shores, where water, air, and earth are joined, but we can hardly see in this a prevision of the theory that the littoral fauna is the most primitive. The Ur-Schleim took the form of microscopic vesicles, or Infusoria, each a spherical aggregate of an almost infinite number of mucous points, and from agglomerations of these vesicles the bodies of plants and animals were formed—a view in which Prof. Hyatt, for instance, sees a prevision of the cell-doctrine. Another doctrine which may be traced back to Oken is that of Recapitulation, a fact which modern critics of the theory would probably note as establishing a further prejudice against it.

George Louis Leclerc Buffon (1707–1788) was the first of the great pioneers of modern evolution doctrine. Reversing Cuvier's change of opinion, he passed from an early belief in the fixity of species to an extreme theory of their mutability (1761–1766), from which he afterwards in some measure reacted. Although frequently quite explicit as to the general idea of evolution, he continually recoiled from his own conclusions, and contradicted himself to avoid contradicting the Scriptures. But it is hard to tell whether this was an expression of ironical humour, or an attempt to temporize between science and orthodoxy, or due to a perception of the difficulty of the problem. His conception of descent was imperfect in so far as he adhered to the linear series expounded by Bonnet, nor did he combine his various ætiological suggestions into a consistent theory; but he is entitled to a very high place in the history, since he asked many new questions if he did not answer them, and because of his anticipation of many important ideas, such as pangenesis, the struggle for existence, artificial and natural selection, and geographical isolation. His most significant contribution to ætiology was his theory that the direct action of the environment produced structural changes which were conserved by heredity.

Pioneers of Modern Evolution Doctrine.

Erasmus Darwin (1731–1802), grandfather of Charles Darwin, expounded in prose and verse a theory of the gradual and natural development of organisms from spontaneously generated primordial forms of great simplicity, endowed with an irritability and excitability which made evolution possible. He extended the conception of the struggle for existence to plants as well as animals, but does not seem to have perceived the vital connection between struggle and progress. Although much influenced by Buffon, he held a different causal theory, emphasizing not the direct influence of the environment, but its indirect effect in evoking functional reactions, which in turn produced modifications. "All animals", he says, "undergo transformations which are in part produced by their own exertions, in response to

pleasures and pains, and many of these acquired forms or propensities are transmitted to their posterity."

Lamarck (1744–1829) worked out with greater care than any of his predecessors a logically consistent theory of evolution. In many ways it closely resembled that of Erasmus Darwin, but there is no evidence that Lamarck was acquainted with his writings. Like Buffon, by whom he was undoubtedly influenced, he passed through a stage of avowed belief in the immutability of species, but, having reached an evolutionary position, he excelled his master in the courage of his convictions and in unwavering consistency. He was one of the first to free himself from the untenable conception of a linear genetic series, and to develop that of a branching genealogical tree (1809). In regard to the factors of evolution, he agreed with Buffon and differed from Erasmus Darwin as to the *direct* influence of the environment upon *plants*, which he believed to be directly modified by changes of soil, heat, light, &c.; on the other hand, as regards animals, he differed from Buffon and agreed with Erasmus Darwin as to the *indirect* action of the environment in evoking changed functional reactions. "Environment", he said, "can effect no direct changes whatever upon the organization of animals. But great changes in environment bring about changes in the habits of animals. Changes in their wants necessarily bring about parallel changes in their habits. If new wants become constant or very lasting they form new habits, the new habits involve the use of new parts, or a different use of old parts, which results finally in the production of new organs and the modification of old ones" (cit. Osborn, 1894, p. 168). As is well known, the fundamental postulate of Lamarck's theory was that changes acquired through functional reaction or direct environmental influence (in the case of plants) were transmissible. This he assumed without seeking to prove it, and apparently without thinking that it required proof.

Lamarck's four laws read as follows:—

I. Life, by its essential activities (*propres forces*), continually tends to increase the volume of every body

which possesses it, and to extend the dimensions of its parts up to a limit which it itself imposes. [The Law of Growth.]

II. The production of a new organ in an animal body results from a new need which continues to be felt, and from a new movement which this need originates and sustains. [The Law of Functional Reaction.]

III. The development of organs and their power of action are always in proportion to the functioning of these organs. [The Law of Use and Disuse.]

IV. All that has been acquired, *tracé*, or changed in the structure of individuals during the course of their life is preserved by generation [heredity], and transmitted to new individuals which proceed from those that have undergone these changes. [The Law of Use-Inheritance.]

Johann Wolfgang Goethe (1749–1832), "the greatest poet of evolution", took into his skilled hands the lyre which Empedocles had tuned, but which, since the time of Lucretius, had given forth no music. Even Erasmus Darwin only wrote prose in verse. We cannot in our partiality repress the futile wish that Goethe had loved poetry less and science more, since his was certainly one of the greatest intellects that has ever dealt with evolution problems. Profoundly influenced by the Greeks, by the *Naturphilosophie*, and by Buffon, he remained unfortunately ignorant of Lamarck, just as the latter was unaware of Erasmus Darwin, all of which seems strange to us to-day, when a professor in a small university town in Germany can scarce give a lecture of moment without its being echoed through three continents. Although Goethe was a thoroughgoing evolutionist, combining the theories of Buffon and Lamarck, his main contribution to ætiology was in great part indirect, through his development of the principles of morphology. He placed the theory of homologies on a securer basis, and elaborated the conception of "unity of type" (1796), which has had such a persistent influence on morphological studies. Goethe was also one of those who see in evolution an expression of laws of growth, and seem to have hold of some idea

which they cannot make clear enough to win conviction from their fellows.

Gottfried Reinhold Treviranus (1776–1837) shares with Lamarck the credit of coining the useful word *Biology* (1802), and is chiefly noteworthy for his analysis of the relations between organisms and their environment. He had in some measure that vivid realization of the interactions in nature which was so characteristic of Charles Darwin, and attained to a firm grasp of some other important biological ideas, such as compensation of growth, functional modification, environmental modification, the relation between fecundity and struggle, environmental elimination, and so on. On the other hand, he weakened his general evolution idea by accepting the myth of occasional spontaneous generation even in higher forms of life. Occasionally Lamarckian, he believed especially in the modifying influence of environment, and the following sentence is representative:—"In every living being there exists the capability of an endless variety of form-assumption; each possesses the power to adapt its organization to the changes of the outer world, and it is this power, put into action by the change of the universe, that has raised the simple zoophytes of the primitive world to continually higher stages of organization, and has introduced a countless variety of species into animate nature".

Etienne Geoffroy St. Hilaire (1772–1844) was a pupil of Buffon and a colleague of Lamarck, and like so many of his contemporaries was greatly influenced by Schelling. As a champion of the "unity of plan" doctrine he engaged in a famous argument with Cuvier before the French Academy of Sciences (1830), in which the progressive party was for the first time defeated. Following Buffon rather than Lamarck, he maintained the importance of environmental modifications and believed in their transmission, but his most distinctive doctrine, to which he was probably led by his studies in teratology, was that great changes might be brought about suddenly, as it were by leaps and bounds in development. By this anticipation of what is now called saltatory evolution or discontinuous variation he was

able to suggest an answer to two difficult questions—How are intermediate links so often absent? and how are new types kept from the blending effects of interbreeding?

Robert Chambers (1802–1871), the anonymous author of *Vestiges of the Natural History of Creation* (1844, 10th ed. 1853), expounded the evidences of evolution forcibly, though not always accurately, and sought in the environment not only the immediate prompting cause of modification, but the agency which directs and limits the progressive impulse with which he supposed all life to be endowed. He was well acquainted with contemporary writers, and expresses a combination of Buffon's and Geoffroy St. Hilaire's emphasis on environmental modification with Aristotle's doctrine of a perfecting principle.

As Darwin's brother remarked, the idea of natural selection is logically so simple that "someone must have thought of it before". And we have seen that it was at least hinted at by various writers from the time of Empedocles. It is necessary, however, to distinguish between the mere recognition of elimination and the working out of the idea of selection as the mechanism of progressive adaptation. The whole credit of developing the idea of selection into a complete working hypothesis belongs to Darwin and Wallace, though they were undoubtedly and avowedly anticipated as regards the suggestion of the idea.

Thus Darwin notices the paper read by Dr. W. C. Wells in 1813 and published in 1818, in which the idea of natural selection is clearly applied to races of mankind and to the origin of single characters. Darwin also recognizes that Patrick Matthew, who hid his treasure in an appendix to a work entitled *Naval Timber and Arboriculture* (1831), "clearly saw the force of the principle of natural selection". The idea is also said to have been anticipated by Etienne Geoffroy St. Hilaire, and by the veteran French botanist Charles Naudin (1852).

Darwin did three chief services to evolution-doctrine. (*a*) By his patient, scholarly, and pre-eminently fair-

minded marshalling of the "evidences" which suggest the doctrine of descent he won the conviction of the biological world. He made the old idea current intellectual coin. In so doing he was greatly aided by Spencer and Wallace, Hæckel and Huxley. (*b*) He applied the conception to various sets of facts, such as the expression of the emotions, and the descent of man, and showed what a powerful organon it was. Here again he was greatly aided by his contemporaries, and Spencer's work in this direction is even more important than Darwin's. (*c*) At the same time as Alfred Russel Wallace he promulgated the theory of natural selection—a generalization second in importance only to the general doctrine of evolution. It may be briefly stated as follows:—

Darwinism.

Offspring very frequently differ from their parents in possessing some new feature or variation. In other words, there is something novel in the expression of the inheritance. The reasons for this are obscure, but as to the fact of the frequent occurrence of variations there is no doubt.

In the course of nature there is a manifold struggle for existence, due to a variety of causes, such as the tendency of population to outrun the means of subsistence, or the inconstancy of external conditions. As the result of this struggle, only a small percentage of the organisms born become adults or reproductive. In this process of elimination there will tend to be a weeding out of those with relatively less fit variations, and a survival of those with relatively more fit variations.

Moreover, the favourable congenital variation possessed by the survivors is handed on in inheritance to their offspring, and tends to be intensified when the new generation is bred from parents both possessing the happily advantageous character.

The natural elimination of the relatively less fit variants, or, what comes to the same thing, the natural selection of the relatively more fit variants, explains the transformation and adaptation of species, and the general progress from simpler to higher forms of life.

Darwin held that "natural selection has been the

main, but not the exclusive" factor in evolution, the origin of variations being always assumed. To a certain extent, however, he believed in the inheritance of acquired characters, and agreed with Buffon and Lamarck in recognizing the evolutionary importance of the modifying influences of function and environment.

After the publication of the *Origin of Species*, there was a period of keen and often bitter criticism on the one side, of exposition and corroboration on the other. Spencer and Hæckel gave generalized expression to the more concrete arguments of Darwin and Wallace, and Huxley formed the cutting edge of the new Biology. None the less, the Darwinian theory had a stern struggle for existence before its survival was assured. For a time the question at issue was one which is now almost out of date—the question between evolution and non-evolution, and during this period the evolutionists allowed their differences of opinion in regard to the factors to sink into relative unimportance in their endeavour to present a united front against the wide-spread opposition to the whole idea. But as the intensity of criticism waned, the various schools of evolutionists began to assert their particular creeds. The majority, perhaps, were on the whole Darwinian, sometimes tainted with "Lamarckian heresy"; a minority reverted almost completely to Lamarck's position; others maintained the importance of more or less unknown laws of growth; and a few cautious spirits were convinced evolutionists, but agnostic as to the factors. It may be said that within ten years after the publication of the *Origin of Species* all the diversity of opinion which confronts us to-day was either clearly expressed or existed in rudiment.

Conflict of Opinions.

If we extend our survey on to "the coming of age" of the Darwinian theory, and then take a cross-section of opinion, we find serious opposition to the general idea of organic evolution fast approaching a vanishing point, but the tissue of evolution theories as heterogeneous as before. Three main schools may be distinguished.

First, there is the predominantly Darwinian school,

tending more and more to emphasize the all-sufficiency of natural selection operating upon spontaneous variations. To the main doctrine Darwin himself added his subsidiary theory of Sexual Selection, a particular case of Natural Selection, which his colleague Wallace refused to accept. To the latter, however, it seemed necessary to confess the inadequacy of Natural Selection to explain the higher qualities of man, and he postulated waves of spiritual influx to help the material world over this and other obstacles in its course, a position which, to Spencer for instance, seemed an unwarranted loss of faith in science. But Spencer again was no strict Darwinian, remaining, like Hæckel and others, a firm believer in Lamarckism. Most important, however, was an addition to the Selection theory, suggested by several naturalists, such as Wagner, but brought into prominence by Romanes and Gulick, the theory of "Isolation", without which the divergence of species from a common stock is inexplicable. Isolation is a general term for various processes which tend to restrict the range of intercrossing with a species, and to bring similar variants to pair together.

Another position is that of the Lamarckians and Buffonians, who emphasize the transforming power of function (use and disuse) and of changed environment (all manner of surrounding influences), and believe in the transmission of acquired characters or modifications. They are sometimes, though not elegantly, called "transmissionists". The school has found its chief supporters in France, where Lamarck in his lifetime got such scant justice, and in America, where it seems to be in the ascendant. It must be noted that not a few, *e.g.* Hæckel and Spencer, combine a belief in modification-inheritance with a selectionist position.

The doctrine of the Lamarckian and Buffonian school owes its strength to the fact that an individual organism is certainly influenced by what it does or does not do, and is plastic in the grip of its surroundings; its weakness is in the absence of evidence to show that the modifications or bodily changes so acquired are in any degree transmissible from parents to offspring. It was

perhaps a recognition of this weakness that led Darwin to leave Lamarckism more and more out of account as he grew older, and it is a recognition of this weakness that has led Prof. Ray Lankester to say that perhaps the greatest step of progress in modern ætiology will be the complete removal of all taint of Lamarckism.

As we shall see later on, a recent suggestion has made it possible to retain an evolutionary, as opposed to a merely physiological interest in modifications, even although their transmission is denied.

In 1866, when Hæckel's *Generelle Morphologie* was published, Cope and Hyatt independently stated certain evolutionary ideas which were afterwards developed into what is often called Neo-Lamarckism. The former based his conclusions primarily on a study of Amphibia, the latter on a study of extinct Cephalopods, and they agreed that the variations which result in evolution "are not multifarious or promiscuous, but definite and direct".

The Neo-Lamarckian school, which might perhaps be called Nägelian, includes those to whom the evolution of organisms is pre-eminently a story of growth, of progressive variation in definite directions. Their contention, phrased in many different forms, seems to amount to this: that the nature of the organism is self-differentiating and self-integrating, that its very nature implies self-adaptation and a potentiality of progress, that its racial growth tends to be cumulative, selective, determinate, and harmonious like crystallization. This school has never commanded attention as the Darwinians and the Lamarckians have done, partly, perhaps, because its members have so often lost themselves in what seems to outsiders mere meaningless babbling, not unnatural, perhaps, since our knowledge of the nature and conditions of growth is so infantile. But while it is easy to scoff at the verbalism of this school, and to nickname them "Topsians" for the naïveté of their discovery that the cosmos *grows*, there was behind their verbalism and naïveté, as Nägeli's work well shows, a firm grip of the idea—perhaps Utopian—that a complete ætiology must carry on the laws and lessons of the inorganic to a solution of the problem of organic evolution.

If we take a third cross-section, namely, at the present day, we find the same diversity as heretofore, but, just as in sections of a developing embryo, the several components are beginning to be more sharply differentiated. The Neo-Darwinians are more thorough-going selectionists than Darwin was, and the Neo-Lamarckians have added breadth and subtlety to Lamarckism. There are still a few who try to put back the hands of the intellectual clock; but the vast majority would agree with Wallace (1889), that "Darwin did his work so well that 'descent with modification' is now universally accepted as the order of nature in the organic world". By its applicability to many different orders of fact, and its continual fruitfulness in research, the evolution-concept justifies itself more and more completely as a *modal* interpretation of the world around us, and is fast becoming organic in all our thinking. At the same time, while conviction has deepened, the early dogmatism has disappeared, for the consistent evolutionist recognizes that he and his interpretation, like the world which he studies, are within the sweep of the evolution process, have been evolved, and are still evolving. Therefore he is far from claiming finality of interpretation, for that would be a self-contradiction.

But while the *fact* of evolution forces itself upon us, certainty in regard to the *factors* seems as far off as ever. When we remember the complexity of the problem and the relative youthfulness of serious ætiology, the recognition of uncertainties is seen as a symptom rather of progress than of any disruption, or perhaps as analogous to that histolysis which often precedes organic metamorphosis. And, we would reiterate, the uncertainties affect the *method* of evolution—its causes, its factors—in nowise the stability of the general idea.

Among the steps of importance which have been taken of recent years, the following appear outstanding:

Some Recent Steps. (*a*) Weismann's supplement to Darwinism; (*b*) Bateson's study of variation; (*c*) the statistical studies of Weldon, Pearson, and others; (*d*) the inquiry into modes of Isolation; and (*e*) the theory of "organic selection".

(*a*) As we have seen, the great gap in Darwinism is the absence of a theory of variation. It is assumed that there has been a continual crop of variations—usually spoken of as fortuitous, indefinite, and small in amount—on which the sickle of natural selection has operated. As to the causes of the crop nothing is said—Darwin simply confessing that the problem was beyond his powers of solution. To Weismann, however, belongs the credit of having taken several bold steps into the darkness. For a time Weismann emphasizes the evolutionary interest of the ancestral Protozoa, which, being more liable to external influences than the higher creatures are, were supposed to have accumulated a sufficient stock of qualities or possibilities to account for all the apparent new departures on the part of their descendants. All variations among Metazoa, in short, were regarded as combinations and permutations of what the Protozoa had acquired.

Then, for a while, Weismann emphasized *amphimixis*—that mingling of qualities which occurs in fertilization at the origin of each new life; and again he added to this another source of change prior to fertilization, namely, in the reducing divisions which take place in the maturation of the ovum, or in the course of spermatogenesis.

Of late, however, Weismann has spoken more frankly in regard to yet another source of variation, although that involved in amphimixis and reducing-divisions is still recognized. He speaks of the primary constituents of the germ having a certain scope for variation among themselves, and supposes a struggle of parts not only in the body, as Roux did in his famous *Kampf der Theile im Organismus*, but in the germ. There is an intra-germinal struggle and selection.

But much more than this. He says: "We are undoubtedly justified in attributing the cause of variation to the influence of changed external surroundings". This means that a change within an animate system must be traceable in the long-run to a change in the larger system of which the organism forms a part, and that certain big environmental changes, *e.g.* of climate

and nutrition, may operate through the body on the germ, acting as stimuli on its variable primary constituents. This does not amount to saying that changes on the body can, *as such*, affect the germ and become transmissible; and the dominant idea of his Romanes lecture is, furthermore, that we call environmental forces efficient causes of change when we are only warranted in calling them stimuli.

Thus, as causes of variation, Weismann has suggested:—

(1) The influence of the environment on the germ-plasm of the primitive Protists.

(2) The permutations and combinations of vital substances and qualities involved in the processes of maturation and fertilization.

(3) The stimuli of nutritive and other environmental conditions upon the germ-plasm within the body.

The most recent and the most subtle of Weismann's theories bears the title "germinal selection". It is a suggestive hypothesis, but difficult to state in a few lines. All are familiar with the Darwinian concept of the struggle for existence, and the selection or elimination of individuals; Roux and others have elaborated the idea of a struggle of parts within the organism and of a corresponding intra-selection; there is also often a struggle among potential ova and among possibly effective spermatozoa; but Weismann, after his manner, has carried the selection idea a step further, and has pictured the struggle among the determining elements of the germ-cell's organization. It is at least conceivable that the stronger "determinants", *i.e.* the particles embodying the rudiments of certain qualities, will make more of the food-supply than those which are weaker, and that a selective process will ensue.

Let us suppose a case in which, through congenital variation, a structure is undergoing gradual degeneration; the germinal aspect of this *may be* that the determinants corresponding to the structure in question are weak in the germ-cell; but as the result of the germinal selection they will tend to be further weakened, until, indeed, they disappear.

There is not any obvious way of proving or disproving an ingenious hypothesis of this sort, but it is in line with the central idea of Darwinism. If a process of germinal selection can be admitted as aiding and abetting the processes of selection at higher levels (intra-selection and individual selection), a new strength is given to the general selectionist position.

(*b*) Mr. Bateson's great work, entitled *Materials for the Study of Variation*, is an endeavour to get out of the speculative mire in which, to the physicist's contempt, the biologist still flounders. It is an attempt to get beyond the vagueness of the assumption that "variability exists" to a sure knowledge of what variations do actually occur. Life is so abundant and so protean that we draw cheques upon nature almost *ad libitum*, and in our impetuosity scarce wait to see whether they are honoured.

By an examination of specimens in many collections and museums, by detailed investigations in regard to particular cases of importance, and by careful sifting of recorded instances of variation, Mr. Bateson has given us a sound foundation upon which to build. It must be noted, however, that he has as yet confined himself almost entirely to one kind of variation, which he terms *meristic*, *i.e.* variations in the number, symmetry, and arrangement of parts. He leaves to a future volume almost all discussion of *substantive* variations, that is to say, changes in quality and substance, which to most biologists are probably of greater interest. Many of the variations with which he deals, such as branched legs in insects, are not of the sort which we suppose to have furnished the raw material of evolutionary progress. In fact, they are too "monstrous".

As is well known, the ordinary, though not universal, conception of the process of organic evolution is that from an ancestral form by minute and, at first, almost insensible differences a new form arises. The minute variations may be indefinite and indeterminate, as most Darwinians follow their master in believing; or they may be definite and determinate, along particular lines, as is suggested from many sides, by Lloyd Morgan with

his crystals, by Galton with his finger-prints, by Geddes with his flowering plant, by the palæontologists (Cope, Hyatt, &c.) with their shells and teeth, and so on.

But, apart from the question of definiteness or indefiniteness, the general view is that of *a continuous series of minimal variations*, from which Darwinians believe that natural selection has brought about the observable discontinuity of species.

Now one of the results of Bateson's work is to create a presumption in favour of a belief in *discontinuity of variation*. "The discontinuity of which species is an expression has its origin, not in the environment, nor in any phenomenon of adaptation, but in the intrinsic nature of organisms themselves, manifested in the original discontinuity of variation." "The existence of new forms, having from their first beginning more or less of the kind of perfection that we associate with normality, is a fact that disposes, once and for all, of the attempt to explain all perfection and definiteness of form as the work of selection." It should here be noted that Mr. Galton also has repeatedly expressed his belief in the occurrence of what he calls "transilient" variations, and has adduced some evidence in support of his position.

Mr. Bateson's main induction is that variation is frequently discontinuous and large in amount, and his suggestion, like that of Geoffroy St. Hilaire, is that the variations which have been important in the origin of new species may have been *discontinuous* in their nature. Thus he does not believe that natural selection has played such an important rôle as the Darwinians suppose, and require to suppose. In short, discontinuity of species results from the discontinuity of variation, and does not primarily depend upon selection.

Furthermore, his induction discloses a greater definiteness of variation than is suggested by the words "fortuitous", "indefinite", "in every part of the organism" used by the Darwinians to describe the variations which they assume. Mr. Bateson suggests that this definiteness is an expression of the physical limitations put upon variation by the conditions of organic stability.

To this the extreme Darwinians would probably answer that this characteristic of organisms—to assume a new equilibrium when the old one is disturbed—is itself the result of a selective process which has been at work since the very beginning of life.

One of the most important criticisms which Bateson brings forward may be briefly stated as follows. Species are discontinuous; how? The Lamarckians and Buffonians answer: by the accumulation of structural responses to the conditions of the environment; the Darwinians answer: by the natural selection of particular terms in a continuous series of minimal variations, the selection being determined in relation to the surrounding conditions or environment. In both cases it is a question of relation between the organism and the environment. But whereas species are discontinuous, the conditions of the physical environment tend to form a continuous series, that is to say, different environments pass insensibly into one another. Moreover, different species occur in similar environment, and members of the same species inhabit different environments. To this dilemma Bateson's answer is, of course, that discontinuous variations occur which are neither direct nor indirect adaptations to the environment; while the Darwinian answer is that an essential part of an organism's environment is animate, namely, the surrounding organisms which are discontinuous or specific. But this Bateson would doubtless call a vicious circle, as the original discontinuity is what has to be explained. On the other hand, one wonders if there is not a tendency to exaggerate both the discontinuity of species and the continuity of the environment.

Inter alia, Mr. Bateson refutes the common belief that variation is greater in amount in domesticated animals than in wild forms; and he also combats the hypothesis of Reversion, which is conveniently appealed to to explain the sudden occurrence of large and regular variations.

Within our limits we are unable to give more than a hint of the scope of a work which seems to us one of the most important contributions to evolution doctrine

since Darwin's day, but we have said enough to show that Mr. Bateson has made an important step towards reaching solid ground, and a timely protest against attempting to give a false appearance of simplicity to the intricacies of nature.

(*c*) *Statistical Study of Variation.*—The application of statistical methods to the study of variation may not sound very attractive to the outsider, and yet if he take the trouble to read Prof. Karl Pearson's essay on the relative variability of man and woman he will find how important the method is in regard to conclusions which he cherishes or abhors.

The statistical method measures a selected character—in man or crab, in buttercup's petals or sparrow's egg—and after a sufficiently wide survey plots out a curve showing the amount of variation which occurs and the proportionate number of variants on either side of the average.

If curves be constructed for individuals of different age, it may be shown that there is a greater death-rate among the variants on one side of the average than on the other, and this leads on to a measurement of the action of natural selection.

Of course there are many difficulties in the use of the method and in the interpretation of the results, but what concerns us here is that Mr. Galton, Prof. Weldon, Prof. Pearson, and others have introduced a method of measurement into a domain where certainties are few and platitudes many.

(*d*) *Isolation.*—A formidable objection to the Darwinian theory, first stated by Professor Fleeming Jenkin, and often urged since, is that particular variations of small amount would tend to be lost or neutralized by intercrossing. In artificial selection the breeder takes measures to prevent this—by isolation; but what is the factor in natural conditions?

The usual Darwinian answer to the difficulty is to suppose that numerous similar variations occur at once. Thus Weismann says, "The necessary variations, from which transformations arise by means of selection, must in all cases be exhibited over and over again by many

individuals". But one fails to find as yet sufficient warrant for this supposition that numerous similar, fortuitous, indefinite, indeterminate variations should occur. For Lamarckians, or for believers in progressive variation along definite lines, the supposition is natural, but not for Darwinians.

Another answer to the difficulty—applicable to certain cases—might perhaps be found in the fact, which breeders allege, that certain strongly marked (germinal and racial) variations are by no means readily swamped, even in the absence of isolation. We might perhaps venture to speak of a struggle for existence within the fertilized ovum, wherein the physical basis, corresponding, let us say, to a strongly marked paternal characteristic, asserts itself even without co-operation from the maternal substance.

But the answer which has been within recent years suggested by Romanes, Gulick, and others is an elaborate theory of "Isolation". Under this title they include a variety of ways in which free intercrossing is prevented between members of a species, *e.g.* by geographical barriers, by change of habit, by a reproductive variation causing mutual sterility between two sections of a species living on a common area, and so on.

According to Romanes: "Without isolation, or the prevention of free intercrossing, organic evolution is in no case possible. Isolation has been the universal condition of modification. Heredity and variability being given, the whole theory of organic evolution becomes a theory of the causes and conditions which lead to isolation."

There is still, however, a lack of sufficiently precise evidence in regard to the supposed swamping without isolation, and in regard to the supposed general prevention of free intercrossing.

(*e*) *So-called "Organic Selection"*.—Prof. Weismann suggested in one of his essays that individual modifications, though not transmissible, might co-operate with progressive congenital variations in effecting adaptations of importance, and this hint has been developed by Prof. C. Lloyd Morgan, Prof. Mark Baldwin, and

Prof. H. F. Osborn, who have independently suggested an ingenious theory as to the possible evolutionary interest of modifications. To this theory the unfortunate title "organic selection" has been given.

There are many facts which show that the body of an organism may react adaptively to changes in function and environment; the skin may be hardened, a muscle may be strengthened, even a bone may be modified. These modifications are obviously of individual value, but if they are not in any degree transmissible they are not of *direct* racial value. It may happen, however, that a congenital variation occurs in the same direction as the adaptive modification, and if the modification be of importance—of value in deciding survival—it may act, so to speak, as a shield for the incipient congenital variation until this has gained strength. The two processes of modification and variation will thus help one another.

As Prof. Lloyd Morgan puts it: "Any congenital variations similar in direction to these modifications will tend to support them and to favour the organism in which they occur. Thus will arise a congenital predisposition to the modifications in question. The longer this process continues, the more marked will be the predisposition, and the greater the tendency of the congenital variations to conform in all respects to the persistent plastic modifications; while the plasticity still continuing, the modifications become yet further adaptive. Thus plastic modification leads, and germinal variation follows: the one paves the way for the other."

In short, it is suggested that "the modification *as such* is not inherited, but is the condition under which congenital variations are favoured and given time to get a hold on the organism, and are thus enabled by degrees to reach the fully adaptive level".

Conclusion.

What can one say in conclusion, except this, that while the general conception of evolution stands more firmly than ever as a reasonable modal interpretation of nature, there is great uncertainty in regard to almost every question concerning the factors in the evolution process.

Thus, what is the relative frequency of continuous and discontinuous variations? In what proportion are observed variations merely individual or possibly racial? What are the causes of germinal variations? Are somatogenic modifications *in any degree* transmissible? What is and has been the scope and rigour of natural elimination? To what extent is isolation demonstrable? These and a score of similar questions are at present unanswerable.

It is not that we are where we were forty years ago. It is rather that we have become more aware of our ignorance and of the complexity of the problem.

Easy enough it is to express *opinion*, *e.g.* that there must be something after all in the Lamarckian and Buffonian position, though one is at a loss to explain the mechanism of heredity whereby modifications of the body could be transmitted; that many, from Geoffroy St. Hilaire to Bateson, have shown evidence for leaps and bounds in evolution; that Nägeli, Eimer, and a dozen others have been on the track of undiscovered laws of progressive growth; that Darwin and Wallace were right in insisting on the importance of natural elimination, though it may not be so all-sufficient as is often supposed; that Romanes and Gulick disclosed a new factor in expounding the various forms of "isolation"; that Weismann has done well to expose the credulity of belief in the inheritance of acquired characters, though he may have exaggerated the negative position; and that the same naturalist's hypotheses as to the origin of variations are at present most welcome stop-gaps in our ætiology. But *opinion* has no place in science.

It is then a *thätige Skepsis* which appears the healthiest mood at present. Not of course that this is anything new; it is a constantly recurrent phase, alike in the individual and in the race. Indeed, the rate of intellectual progress in either may perhaps be measured by the more or less rapid recurrence of the sceptical phase.

Lamarckianism was in its way a very satisfactory theory—until its weak points were discovered; Darwin went, though in another direction, one better; Weis-

mann has gone one better still. One must pass through these stages and appreciate their strength before one sees their weakness, and becomes, at each transition, a sceptic of a higher order. It is difficult to abbreviate the intellectual ontogeny, except in the course of generations. Thus, Weismannism seems vanity and vexation to those who have never found the limits of Lamarckianism, nor strained at the Darwinian tether. Undoubtedly the various stages will seem larval enough some day.

But to all who have tried to sound the depths—not altogether pellucid—of modern ætiology, one result at least should be clear—that we need to get back to facts. We fully recognize the value of speculative interpretation, of logical dialectics, even of controversy—with what Spencer calls "its terrible fertility, and unmanageable population of issues, old and new, which end in being a nuisance to everybody"; but periodically there must be a re-examination of the basis of fact. Perhaps Weismann's *greatest* service after all, and in part because of the masterliness of the theory, will be in forcing biologists back to experiment.

It seems needless to suggest that there should be a pause in speculation. For we need all the suggestions we can get, and the intellectual speculator will not be discouraged whatever one may say. At the same time, it becomes tiresome to wade through the flood of ætiological literature when one observes how much of it might have been spared us, if the writers had only read the *Origin of Species* more carefully, or taken the trouble to understand Weismann.

It is also fair to recognize that there has already been a fair amount of experimenting. But relatively little of it has had any direct reference to the factors of evolution. It is recognized on all sides that what we now require is a period of experimental evolution.

Among the lines of observational and experimental work which are open or have been opened, the following may be noted:—

(1) Experiment and observation on the nature of variations (*e.g.* Bateson's work).

(2) Experiment and observation as to the causes of variations.

(3) Experiments on the influence of surroundings (see Semper, &c.).

(4) Experiments on the influence of function (see H. de Varigny's *Experimental Evolution*; Arbuthnot Lane on the *Anatomy of the Shoemaker*).

(5) Experiments on amphimixis (see the records of the Breeders and Cultivators).

(6) Experiments on heredity (*e.g.* Cossar Ewart on Telegony).

(7) Experimental Embryology (*e.g.* the work of Roux, Hertwig, Driesch, Herbst, Wilson, &c.).

(8) Experimental Psychology (*e.g.* Lloyd Morgan on chicks, &c.).

(9) Experimental Bionomics (*e.g.* Stahl on snails).

As to the mood in which this work should be done—and it will require centuries—we can find no finer expression than Mr. Bateson has given in the preface to his *Materials for the Study of Variation*.

He heads his work with the familiar words: "All flesh is not the same flesh; but there is flesh of men, another flesh of beasts, another of fishes, and another of birds", and says, "I have there set in all reverence the most solemn enunciation of the problem that our language knows. The priest and the poet have tried to solve it, each in his turn, and have failed. If the naturalist is to succeed he must go very slowly, making good each step. He must be content to work with the simplest cases, getting from them such truths as he can; learning to value partial truth, though he cheat no one into mistaking it for absolute or universal truth; remembering the greatness of his calling, and taking heed that after him will come Time, that 'author of authors', whose inseparable property it is ever more and more to discover the truth, who will not be deprived of his due."

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